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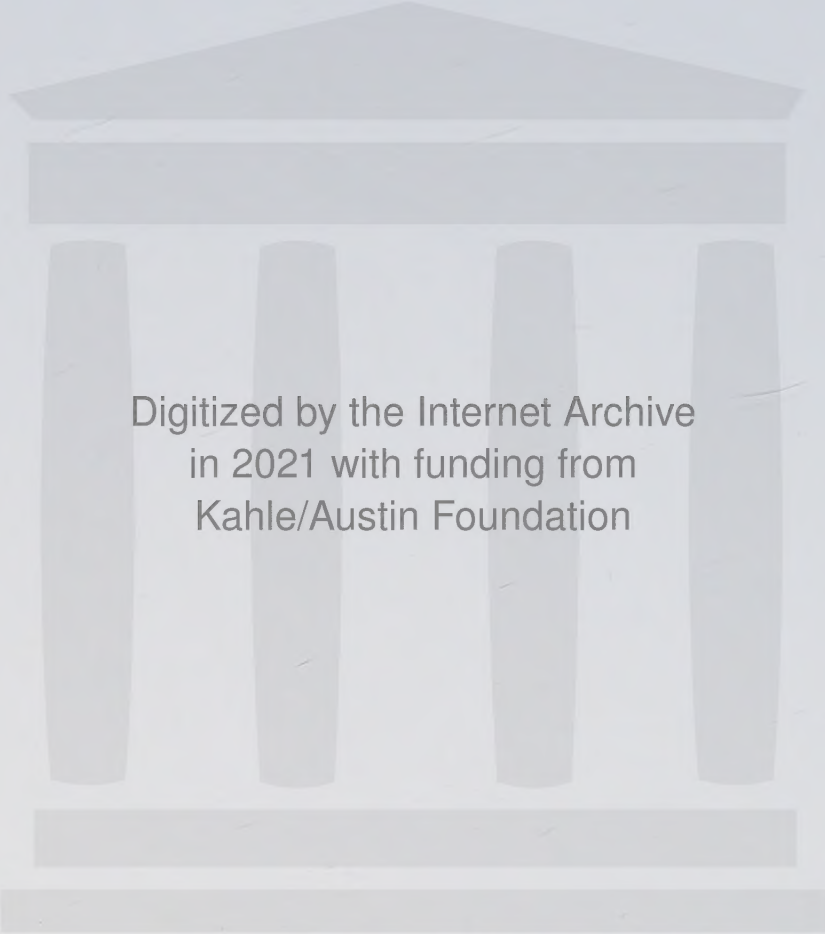
Parasitic Wasps

Evolution, Systematics,
Biodiversity and Biological
Control

Ed. by George Melika and Csaba Thuróczy



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PARASITIC WASPS
EVOLUTION, SYSTEMATICS,
BIODIVERSITY AND BIOLOGICAL CONTROL

George Melika & Csaba Thuróczy
(editors)

Ministry of Agriculture and Regional Development
Central Service for Plant Protection and Soil Conservation
Plant Protection and Soil Conservation Service of County Vas
Systematic Parasitoid Laboratory

PARASITIC WASPS

EVOLUTION, SYSTEMATICS,
BIODIVERSITY AND BIOLOGICAL CONTROL

George Melika and Csaba Thuróczy
(editors)

International Symposium:
"Parasitic Hymenoptera: Taxonomy and Biological Control"
(14–17 May 2001, Kőszeg, Hungary)



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FOREWORD

The idea of this book originated from discussion held among members of the organising committee for the international symposium "Parasitic Hymenoptera: Taxonomy and Biological Control", held in Kőszeg, Hungary in May 2001. The symposium attracted many international researchers in their fields. Nearly all the papers and posters presented at the symposium appear in this volume, although many have been substantially modified and improved compared with the original symposium presentations. All the submitted papers were accepted by the editors. All of them have been refereed using the guidelines that generally apply to the scientific journals. The editors have organized the papers into related topics. The book starts with reviews on the current state of biological control in Hungary and taxonomy of Hymenoptera. We hope this volume will stimulate further research in parasitic wasps among students of the Hymenoptera.

George Melika & Csaba Thuróczy

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The editors would like to thank all the staff members of the Systematic Parasitoid Laboratory, colleagues from the Plant Protection and Soil Conservation Service of County Vas (Tanakajd), Central Plant Protection and Soil Conservation Service (Budapest) for their essential efforts in organizing the symposium.

We also thanks many people for their constructive comments on the structure of the book and several sections and the authors for their cooperation and patience when the editors insisted on many and last minute changes.

George Melika & Csaba Thuróczy

CURRENT STATUS AND HISTORY OF BIOLOGICAL CONTROL IN HUNGARY

István EKE

Ministry of Agriculture and Regional Development
Department for Plant Protection and Soil Conservation

At the end of the 20th century, the significant technical development resulted in the coming up of plant protection products to be used for the control of plant pathogens and pests. Disadvantages of the very wide and often unjustified applications have shown their harmful effects. The efforts aiming at reducing the chemical burden on the human environment helped to discover the importance of organisms living in the natural environment, which, in turn may play a great role in the protection of plants by decimating the pests of cultivated plants.

Study and discovery of the complicated host-parasite relations started already in the 1800s, resulting in a slight possibility for biological control. First, in 1855, an American entomologist, Fitch proposed to establish the natural enemies of introduced pests, but the practical use started only in 1873 with the trial of Planchon and Riley to establish *Tyroglyphus phylloxerae* in France from the USA for the control of phylloxera introduced a little earlier. A year later ladybirds were introduced from England to New Zealand for the control of aphids and many other experiments followed all over the world – with more or less successes.

In Hungary, regular research on the pests of cultivated plants started in 1880, when, for the control of the very destructive phylloxera having appeared in our country in 1874, the Ministry of Agriculture set up the National Experimental Station for Phylloxera. It was the first institution in Europe established for the research of insect pests. The new institute was headed by the internationally acknowledged dr Géza Horváth who succeeded in solving the phylloxera problem in Hungary in a period of 10 years. Research work of the station covered all animal and plant pests of grapevine.

As a result of the successes, the scientific activity of the station was extended to the pests of agriculture and forestry, and, in 1890, the new name also changed for Hungarian Royal State Station for Entomology. Biological control experiments already started in the 1890s. In its publication appeared in 1895, the Station reported on the control trials made, under the supervision of dr Géza Horváth, against *Lymantria monacha* in Transylvania in 1892. In order to reduce the pest population, the bacterium *Flacheria* was used. This method was first used in Hungary – and with great success. The report also mentions that the caterpillar of *L. monacha* could not be inoculated with the pathogenic fungus *Botrytis bassiana* because of the low temperature.

In order to learn to conduct trials with the entomophilic fungus, *Beauveria tenella*, Horváth visited Le Moulit in 1891. Back in Hungary, he could start the experiments with the obtained experience and sufficient cultures. The treatments were successful against the larvae of *Melolontha melolontha* and *Rhizotrogus*. Unfortunately, after this promising start, research on the use in practice of the fungi stopped and has been launched again only for the last two decades.

The biological control of mulberry scale (*Pseudaulacaspis pentagona*) and woolly apple aphids, using entomophagues, started with the introduction of *Prospaltella berlese*, and *Aphelinus mali*, respectively. *Pseudaulacaspis pentagona* was introduced from America to Italy in 1885, and

appeared in 1912, very close to the Italian border on the then territory of Hungary, while in 1923 on the actual territory of the country, and must have been introduced with infested propagating materials. As no other control techniques were used with good results, Árpád Jeszenszky brought in twigs infested by parasitized scale insects from Italy in 1926. The material was spread in 54 infested communities. The parasitoid immediately established and the work could go on, in 1927, with materials originating from the place of planting. The pest density was so much lower that the insects occurred only in spots. Even today, the parasitoid plays an important role in controlling the pest, though, recently, the population density of mulberry scale has been more and more increased.

The woolly apple aphids must have been introduced into the Carpatian basin from France in 1875 and became very soon the most threatening pest of apples. Malenotti called Jeszenszky's attention to the fact that good results were obtained with *Aphelinus mali* in the Mediterranean basin. The first consignment of pests arrived from Italy in 1926 and was placed near two apple trees infested by woolly aphids. The following two years, parasitism became so high in the experimental garden that the need for establishing a special laboratory arose for carrying out further tests as well as for producing and distributing propagating materials. The competent authorities, however, misunderstood the situation and therefore the plan failed. Jeszenszky continued to send out propagating materials for another 7 years and succeeded in reducing the infestation by woolly aphids below the damage threshold all over the country. It was confirmed by trials made with *Aphelinus mali* that in case of this parasitoid not only the artificial distribution is very efficient but the spontaneous spread of this species is rather vigorous proving the acclimation capacity of this parasitoid.

The International Plant Protection Convention (NPPC) signed in 1929 in Rome was a milestone in the research of biological agents. As a result of the NPPC, a decree was made in 1932 providing for the merging of the Station for Entomology and the Institute for Plant Pathology and Biochemistry into the Research Institute for Plant Protection. By creating the new institute, the objective was to find a solution for the scientific problems, because the practical plant protection issues were treated by a special organization, the Hungarian Plant Protection Service.

In the 1950s, among the studies on plant-parasite relations made within the frame of the insect ecological research, the discovery of the animal associations of winter wheat by Gusztáv Szelényi and Tibor Jermy was of great importance. During these studies, regular presence of 32 parasitoid *Hymenoptera* and *Diptera*, 6 hyperparasitoid species as well as 5 predators was detected out of 14 insect pest species identified in Hungary.

During the very first decades of the spread in Europe of Colorado potato beetles, trials were made with several natural enemies. In order to find a solution for the greatest agricultural problems of the time, several European countries performed experiments with the most promising and efficient predatory bug, *Perillus bioculatus*. In Hungary, trials started in 1959 in the regional laboratory of the Research Institute for Plant Protection at Keszthely. It was proved that the population spreads rather rapidly, therefore hope for success could be expected by using high density. At an international workshop held in 1962, Tibor Jermy suggested that a joint release experiment should be made at a single place of Europe, therefore a so high population could be established under natural conditions which was not otherwise possible by an individual institute. The proposal was accepted and Hungary was designated for this experiment starting in 1964 and 1965 with the participation of 7 European countries. In spite of the fact that 40.000 and 60.000 *P. bioculatus* larvae were released in the first and second year, resp., the predator could not be

detected in the area. There were several biotic and abiotic troubles hindering the establishment of *P. bioculatus*. They were all confirmed. One of the serious abiotic factors was the presence of the native parasitoid *Hymenoptera*, the *Telenomus sokolowi* (an egg-parasitoid), which greatly decreased the population of *Perillas bioculatus*.

In 1964, trials were made to control *Quadraspidiotus perniciosus* by introducing *Encarsia perniciosi*. It was confirmed that this parasitoid overwinters in Hungary and spreads slowly. It can not, however, stop the spread of the pest alone under the ecological conditions of Hungary. Its importance will be better demonstrated in the integrated pest management.

In 1971 the Plant Protection Service of the Ministry of Agriculture established the “Special Laboratory for *Hyphantria cunea*” for controlling the pest causing damages of economic importance. The objective was to work out efficient environmentally-friendly pest management programmes against this quarantine pest, and in 1973, the scope of activity was extended under the general name Biological Control Laboratory. During the 30 years, the development works have resulted in several environmentally-friendly techniques using biological agents in the pest management practice.

Though promising results were already obtained in the practical use of entomophilic bacterium *Bacillus thuringiensis* by Béla Husz in 1928 and trials were carried out by other countries’ scientists on European corn borer (*Ostrinia nubilalis*) making reference to Husz, this work stopped in Hungary. Forty years later, the new special laboratory focuses on long-term studies with this bacterium, including several variants and sub-species.

In public areas, only *Bacillus thuringiensis* var. *kurstaki* preparations are used to control *Hyphantria cunea*. This bio-preparation is used to control *Ostrinia nubilalis* and *Helicoverpa armigera* in the production of corn seed and sweet corn. On several thousands of hectares, it is widely used in forestry to control *Lymantria dispar*.

In the regions of great ecological concern (national parks, landscape protection zones, surroundings of lakes Balaton and Velence), formulations with *Bacillus thuringiensis* var. *israeliensis* are widely used against mosquito larvae.

The NOVODOR FC formulations containing *Bacillus thuringiensis* var. *tenebrionis* are used to control larvae of *Oulema* species and Colorado potato beetles.

Adaptation and development of biological control techniques used against greenhouse pests have had successes over two decades. The beneficial living organisms are extensively used in the major vegetables grown under greenhouse. Biological methods are widespread mostly against polyphagous pests. First, the application techniques of *Phytoseiulus persimilis* were elaborated to control *Tetranychus urticae* Koch showing less and less sensitivity to miticides, under the Hungarian forced production.

Encarsia formosa and *Eretmocerus californicus* parasitoids are well used to keep the populations of greenhouse whiteflies (*Trialeurodes vaporariorum*) and tobacco whiteflies (*Bemisia tabaci*) below the infestation level. Their action can be improved by introducing the predatory bugs (*Macrolophus caliginosus*).

For the control of aphids, adequate parasitoid species (*Aphidius colemani*, *Aphidius ervi*, *Aphelinus abdominalis*) are established with the so-called “bank-plant method”. If needed, *Aphidoletes aphidimyza* may be established to treat the critical foci in order to improve control safety.

Preventive uses of *Neoseiulus cucumeris* predatory mites are widely spread in the Hungarian practice to control outbreaks of Western flower thrips (*Frankliniella occidentalis*), vector of Tomato spotted wilt virus. At the appearance of the thrips, flower bugs (*Orius insidiosus* and *O. laevigatus*) are released for reducing the number of thrips and virus infection below the damage threshold.

Liriomyza bryoniae with seasonal outbreak is controlled by the establishment of *Diglyphus isaea* and *Dacnusa sibirica* and a reliable management programme is available for the growers.

In addition to working out biological control programmes for arthropods, the Biological Control Laboratory developed microbiological agents (primarily antagonist fungi) to control some pathogens under greenhouse conditions. The formulations containing these agents are registered and widely distributed in Hungary. At present there are three biological agents on the national market and a new one is in the registration procedure.

1. MYCOSTOP (*Streptomyces griseoviridis*) – against diseases caused by soil fungi
2. TRICHODEX WP (*Trichoderma horzianum*) – against *Botrytis cinerea*
3. KONI (*Coniothyrium minitans*) – against *Sclerotinia* spp.
4. PLANTSHIELD (*Trichoderma horzianum*) – it will be available soon to reduce the fungal diseases of the soil.

From 1998, the activity of the Laboratory has been extended with the development of diagnostic methods for quarantine pests. The changed name of the facility is Laboratory for Biological Control and Quarantine Methodology. In addition to development of biological control methods, the laboratory will, therefore, have the task of working out quality control system for, and regular checks of, products containing biological control agents.

According to the global requirements of our era, all efforts should be made to reduce the application of plant protection products, therefore the health of the plants must be protected by using biological agents in the integrated plant production. This phenomenon raises, however, new problems, i.e. the precise and reliable identification of species of the beneficial organisms to be used in biological control. The last two centuries were mostly characterised by the establishment of exotic biological agents, the entomophagues to control the introduced pests. It is unjust that no or very few studies have been made with native entomophagues, because their identification together with that of the very efficient parasitoid species is extremely difficult requiring well qualified expert's skill. Globally, the source of many failures has been the unreliable identification.

Recognizing this problem, the Department for Plant Protection and Soil Conservation of the Ministry of Agriculture and Regional Development established, by 1 January 1998, the Systematic Parasitoid Laboratory, a special laboratory of the Central Service for Plant Protection and Soil Conservation, working at the site of the Plant Protection and Soil Conservation Service of county Vas.

As for the laboratory staff, it was hired from the "Savaria" Natural Science Museum where collecting and identifying activities were first of all made. In order to clarify the significant taxonomical problems (both at national and international levels), faunal research still plays an important role in the activity, but the real objective is to support directly agricultural production. With this in mind, surveys are made purposefully in the agro-ecosystems: parasitism of the agricultural and forestry pests should be studied in each region.

The main tasks are as follows:

- detection and determination of parasitoid species present in the cultivated crops,
- selection of the most effective parasitoid species for biological control,
- study and determination of their biology and host -parasite relations,
- analysis of the pest management programmes of different crops for host-parasite relations,
- study and use of techniques safe for the parasites,
- study of techniques safe for the parasites in the pesticide registration procedure,
- use of molecular biological methods, PCR for identification (taxonomy)

The Laboratory works as a scientific workshop for research and development of Hungarian insect parasitology and, in the future, will become an internationally accepted and recognised centre in this field.

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PART 1

The Hymenoptera: an Introduction



PARASITIC WASP TAXONOMY INTO THE 21ST CENTURY

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Abstract – In this paper I suggest that taxonomy in general, and parasitic wasp taxonomy in particular, are going to change radically in the next few years as a result of both the great advances in molecular systematics and also the inevitable increasing role of the world wide web. I argue that the influence of molecular studies, and especially of DNA sequencing, will increase not only because it is becoming less expensive and quicker (and no doubt will continue to do so) but also because of it's ability to discover and discriminate cryptic species which may be abundant among both parasitoids and their hosts (though the magnitude of the cryptic species problem has yet to be properly estimated). I suggest that where possible, use should be made of existing taxonomic expertise to obtain fresh, well identified material of all taxa for molecular studies. The possibility then of using sequence data in identification is considered with web-based systems is considered. The web also has the capacity to empower taxonomy in parts of the world where access to libraries and to museum type specimens (mostly held in the 'west') is severely restricted. The 21st century will see the seamless combination of web-based and molecular taxonomy.

Introduction

We are commencing on a revolution in taxonomy and in systematics in general, brought about by a combination of factors, and this revolution will be felt most when it comes to the megadiverse taxa such as the arthropods, nematodes and fungi. Even within these, there are some especially poorly known groups, and one such group comprises the parasitoid Hymenoptera which will be the main focus of this article.

The factors leading to the revolution are both good and bad.

- The mismatch between the taxonomic work that lies ahead of us, with the larger part of the earth's biodiversity still undescribed and yet a steady decline in practising taxonomists.
- The molecular revolution with rapidly increasing facility and decreasing cost of DNA sequencing and related techniques, together with the greatly enhanced ability to resolve difficult taxonomic problems.
- The growth of the www and computing power, with its capability of distributing taxonomic information and interactive identification tools to an enormously wide community.

Integration of the above two with intelligent systems that will take the unwanted mystique out of taxonomy and nomenclature, and so link different user communities seamlessly.

Here I will discuss these issues in turn, and offer my view of a not too distant taxonomic future. However, I will also emphasise the great need to continue building collections, indeed re-building in most cases, this time with the key feature being preservation of specimens in such a way as to minimise loss of sequencable DNA and enabling its long term storage.

The taxonomic problem

One major problem is exemplified by the fact that during the quarter of a millenium that has passed since the publication of Linnaeus' *Systema Naturae*, and with it the beginning of modern taxonomy, the taxonomic community as a whole has at most described 50% and more likely only 10–20% of the diversity of life on our planet or even less (Erwin 1982; May 1990; Dolphin & Quicke 2001). If taxonomists continue to work at the same rate and within the same basic framework of making descriptions, identification keys and descriptions, it could well be the next millenium before we have dealt with the world's fauna. Whether there will be much of the fauna left by then is anyone's guess. More pressingly, we have the practical problems of identifying those organisms that are of direct concern to us. These may be pests or beneficial taxa, or they may be the objects of other scientific endeavours such as the construction of food webs that will enable us better to understand community ecology processes (Memmott & Godfray 1994; Godfray *et al.* 1999).

Without doubt, even just taking a morphological species concept we are faced with many problems of identification that are especially acute in the traditionally taxonomically difficult groups such as the parasitic Hymenoptera.

The cryptic species problem

One barely considered aspect of the taxonomic impediment is the possibility that even in those groups that we consider to be well-worked taxonomically, there may be a lot of hidden diversity, in the form of cryptic species. We simply have no idea how many of the species that we currently think that we can recognise are in fact aggregates of two or more cryptic taxa. Equally, because the great majority of taxonomy is based on dead museum/herbarium specimens, of taxa that have hardly or never been observed in life, we don't know much about the converse – that is taxa that we believe at present to be different species but which are in fact members of a single gene pool. Even if the taxa are available alive, interpretation of laboratory crosses and rearings can be very misleading because taxa that can be made to cross and produce viable offspring in the lab, may nevertheless never do so in the wild.

Does recognising cryptic species matter?

One example from the parasitic wasp world should suffice. The widely cultured parasitic wasp, *Anisopteromalus calandrae*, has been the subject of more than 350 biological papers. It is a parasitoid of bean weevils (Bruchidae) and has been especially widely used in population dynamics studies. On a visit to my laboratory at Silwood Park, Dr Vladimir Gokhman, of Moscow State University, and I made a karyotype preparation from an *A. calandrae* from the culture maintained at Silwood Park and found a haploid chromosome number, n , of 7 (Gokhman & Quicke 1995). Subsequent investigation of the Moscow State University culture revealed $n = 5$. After reconfirming these results in case of some inadvertent error (Gokhman *et al.* 1998), the biologies of the two populations were investigated in detail and found to be very different in many ways (Gokhman *et al.* 1999). The Silwood culture was found to show many features typical of an r-selected organism, and the Moscow one displaying typical K-selected features. Further, they had

different host preferences, and the two types could not be got to mate with each other in the laboratory, thus confirming that they belong to different species. Further studies on cultures maintained in several other institutions through Europe and North America, revealed that each species was widely distributed. The differences in biology are so marked that it would be meaningless to try and relate one type of measurement from one species to another from the second. In those cases in which the cultures have been lost since papers were published, and the origins of the cultures are not recorded, it may not be possible to determine which of these two species were actually studied. Morphologically these species are extremely similar, and although some minute, apparently consistent differences have been found, it is unlikely that even an expert would have detected the presence of two species without some other suspicion that there might be something odd going on.

I believe that there is an urgent need to identify a small number of gene fragments that can be reliably amplified and which together will enable identification of species with high fidelity. At present there are unfortunately different genes of choice used by different research groups and on different groups of organisms – a Tower of Babel as Caterino *et al.* (2000) put it. Ideally one easily-amplified gene will be found that will enable a taxon to be placed unambiguously within a small group, such as a subfamily, but more ideally a tribe, and another one or two fragments that will then enable accurate identification to genus level and to a particular species – in this case, a molecular recognisable taxonomic unit. From our own work we have found that within the Ichneumonoidea and the Eulophidae and within the Hymenoptera more generally that the D2+D3 expansion region of the 28S rDNA gene serves the first role very well (Belshaw & Quicke 1997; Belshaw *et al.* 1998; Gauthier *et al.* 2000). This gene region even has some potential at the species level (Laurenne *et al.* 2000; Belshaw *et al.* 2001) but for certain identification more variable genes are required. Two excellent candidates are introns in the elongation factor 1 (EF-1), and the internal transcribed spacer regions (ITS-1 and ITS-2) between nuclear ribosomal genes (e.g. Schilthuizen *et al.* 1998). EF-1 is a highly conserved nuclear coding gene which can be used to investigate recent divergences because it contains fast evolving non-coding introns. ITS regions are similarly non-functional and diverge rapidly between species, but because the nuclear ribosomal gene clusters undergo concerted evolution (they are homogenised with an individual) they tend to show very little intraspecific variation for sexually reproducing taxa. Sanchis *et al.* (2001) has used EF-1 introns to reveal that there are some very good species within the aphidiine braconid genus *Pauesia*, but these often bear little resemblance to morphological species concepts which are based on highly variable, and clearly polymorphic characters such as features of the leg and wing setosity.

Thus DNA data can often be used to solve problems easily that either cannot be sorted out by traditional morphological taxonomy or even if they can, are likely to take inordinate effort. Indeed, it seems likely that only DNA data will be adequate to identify what actually constitutes a species in many cases. Now that molecular approaches are becoming more routine and reliable, and we are getting to know the behaviours of particular gene sequences better, I suspect that we will soon be re-evaluating many of our long-held species notions within the parasitic Hymenoptera and we will then get new insights into host relationships and other variable aspects of biology. Specimens analysed in this way would be assigned to molecular Recognisable Taxonomic Units (mRTUs).

In the next few years we will be faced with a plethora of examples where molecular data have revealed the existence of cryptic species, and because it is probably going to be impossible to be certain about which of any published scientific names relate to which mRTUs, we will either need

a quick, non-argumentative way of just assigning a name to one of them (as with the 1st revisor principle) or we will have to abandon binomial nomenclature in these cases and refer to the species simply by reference to their sequences. Thus, a worker might say that he/she works on the campoplegine ichneumonid whose sequence is X and which attacks the pyralid moth whose sequence is Y – more realistically, the persons will cite accessions numbers in the database where the sequences are stored.

The ecological problems

One of the most worrying things about the biological and ecological literature on parasitoids is that it is replete with errors. These derive from mistakes in the identifications of parasitoids, mistakes in the identifications of hosts, or even both (Noyes 1994; Shaw 1994). Sometimes these result from inadequate taxonomy and sometimes pure incompetence, the result, however, is the same. Whereas with few exceptions real host ranges of the vast majority of parasitoids are unknown, the problem is even greater for the parasitoids of cryptic hosts. This is because of the additional problems that many published records are based on substrate rearings and these are very prone to suggesting wrong associations, and because attempts to rear individual parasitised cryptic hosts often have a high failure rate. And, of course, identification of host and parasitoid larvae found together based on morphology is in most cases unlikely to get beyond subfamily level because of a real lack of characters compounded with a lack of authenticated material on which to base taxonomic studies. DNA sequencing of such associated pairs of taxa however offers a way of resolving this. Laurene *et al.* (2000), for example, used sequence data from a parasitoid larva found feeding on the larva of a tropical wood-boring beetle to unambiguously identify it by comparison with adult parasitoids collected in the vicinity (Fig. 1). In this case, as no doubt it would be in the majority of cases for tropical systems, species-level identification of the parasitoid was not possible because no keys to the species exist – indeed it is quite possibly undescribed. It must be emphasised that using DNA, particularly sequence data, to identify genera and species, i.e. mRTUs, is not the same as being able to reconstruct a phylogeny. With the latter there will always be uncertainty.

Once all of the elements of a system, such as a parasitoid or predator food-web, have been identified at the level of mRTUs, most probably using sequencing, further investigation of the system such as quantifying the strengths of the links, can be carried out with a range of less costly and labour-intensive molecular techniques. Several such methodologies are now being investigated on a variety of systems not just in entomology (e.g. Greenstone & Edwards 1998; Agusti *et al.* 1999; Vaino & Hantula 2000).

The potential of the www and intelligent systems in taxonomy

With the development of the WorldWideWeb and its ready application to the dissemination of taxonomic information, we are now starting on a new and potentially remarkable shift in systematics – a “quiet revolution” as Bisby (2000) put it. The role of the www in taxonomy is expanding rapidly, and recently Godfray (2002) has argued persuasively that the whole of taxonomy should become web-based with new starting dates for the taxonomy of each group following ‘publication’ of the 1st web-based reasons. Further, intelligent systems will enable

[illegible]

Figure 1 Manually aligned partial 28S D2 rDNA sequences including independently collected adult and larva of a one species of braconid wasp (*Shelfordia*AD and *Shelfordia*LA respectively) and members of other genera found in the same region, that was used to demonstrate the utility of DNA for working out host-parasitoid relationships when rearing is difficult (Laurenne et al. 2000)

combination of the skills of traditional systematists, and above all, of alpha-taxonomists, with new knowledge gleaned from molecular studies, in such a way that non-experts will be able both to make correct identifications and to access relevant information – online (see Edwards et al. 2000). The www is allowing an increasing amount of information, including illustrations, about species to

be accessed from all over the world at relatively little cost, and for some groups of organisms it currently enables use of online, often interactive, multiple access keys for identification. Further and perhaps more importantly, the web allows easy access to gene sequence data, allowing it to be obtained from, and deposited in, the linked EMBL/GenBank/DBJ databases. Newly acquired sequences can be searched for in these databases very rapidly using similarity search programmes such as BLAST. For some of the commonly sequenced gene fragments (e.g. CO1, 28S rDNA, 16S rDNA, 18S rDNA) even with the current number of entries, there is usually sufficient data to be able to tell pretty well what major group of organisms your new sequence has come from.

The systems currently being developed will soon do a great deal of the work of the traditional taxonomist by spotting potential confusions due to synonyms, and misspellings, flagging possible sources of confusion, so that the outputs of for example literature searches will be as informative as possible. Thus if a species name is searched for, the systems will be able to collate not just the records that have that name and any synonyms, but also spot if there is potential molecular evidence that there might be cryptic species involved, perhaps suggesting cost-effective ways of identifying them, etc. While this will not do away with the need for taxonomists, it will massively change the way that both taxonomists and non-taxonomists who need taxonomic information will operate.

Implications for museums

One of the main problems to be solved on a broad basis is the collection and handling and databasing of material that will be needed for these molecular studies. Unfortunately, the great majority of museum specimens are unsuitable for DNA sequencing (Quicke *et al.* 1999), or allow only short (insufficiently long) fragments to be amplified (Dean *et al.* 2001), or require special expensive and time-consuming methodologies as used in forensics. And of course, museum curators are seldom happy about the prospect of the specimens in their charge being sampled in an inevitably destructive way. The answer is that we need, urgently, to start new collections of material specifically for molecular studies. Such collections will obviously involve organisms of direct relevance to economic or medical issues, but on a broader scale, it seems to me that we need to take every opportunity, as a community of biologists, to start a new type of museum collection on a similar or even larger scale than that which in the past has led to our grand and useful current museums of dried pinned insects, or papered herbarium specimens. This time the collections need to be stored in a manner appropriate for the long-term preservation of sequenceable DNA.

There can be little doubt that DNA sequencing (and related protocols) will become even more powerful, widespread, and, affordable in coming years, and the number of applications will increase proportionately. The current dominance of the western, developed world with this technology will not last as prices fall, and techniques drop out from the life-time of patents. Thus, we are not dealing here with just an elite aspect of systematics, even though at present it may be that way. It will probably be of even greater import to the developing world that is largely distributed in the more biodiverse parts of the world.

The current generation of taxonomists in the major taxonomic institutions of Europe and North America, has long been in decline – it is no longer the case that even the larger collections will probably have a member of staff with expertise even in major groups of organisms. And although much has been made of the current need for more alpha-taxonomists, it seems unlikely that this declining trend will be reversed. Thus we need to make full use of those experts that we still have – put bluntly, we should endeavour to make best use of their knowledge while we still can. I

therefore advocate most forcefully, the need for all museums to start their own DNA-able collections immediately, at least on a small scale, such that they can start the process of assembling material that can be authoritatively identified by their current staff, albeit with the caveat that there may be cryptic, as yet unrecognised species.

Another aspect that needs to be tackled is that of attitudes to collections, collectors and taxonomists, especially to what can be termed 'once-in-a-lifetime' specimens. With habitat loss and degradation, some of these 'once-in-a-lifetime' opportunities may in fact be the last opportunities to obtain DNA-able material for taxa which, even if not economically important, may have considerable scientific importance – without doubt, at least in terms of reconstructing phylogenies, the more data the better.

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Part 2

Systematics and Evolution



MAAMINGIDAE, A NEW FAMILY OF PROCTOTRUPOIDEA UNIQUE TO NEW ZEALAND

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Abstract – The recently described genus *Maaminga* comprising two new species from New Zealand is placed in the family Maamingidae. One species is common in forest, particularly the *Agathis* forests of the northern part of the North Island. The more robust and stocky species, which is polymorphic for wing size, appears to be associated with coastal scrub and forest, particularly on offshore islands, but is also found in subalpine snow tussock. Maamingidae is nominally placed within the Proctotrupeoidea. It may be related to Diapriidae and Monomachidae but relationships are unclear, partly due to the lack of phylogenetic resolution among the proctropoid families and other Proctotrupomorpha *sensu* Rasnitsyn.

Key words: Hymenoptera, Proctotrupeoidea, Maamingidae, *Maaminga rangi*, *Maaminga marrisi*, New Zealand

Introduction

The first specimen of Maamingidae (= *M. marrisi* Early *et al.* 2001) was discovered in the early 1970s by Annette Walker and Errol Valentine of the then Entomology Division of the DSIR, New Zealand, while sorting a sample extracted from leaf litter of subalpine/montane shrubs from the South Island. They recognised its unusual appearance: the head, mesosoma and wings indicated similarities with the Diapriidae but the metasoma was unlike that of any known diapriid and seemed more to resemble Ichneumonoidea. Unable to place it in any family, they sent it to one of us (L. Masner) for examination. Shortly afterwards a second species (= *M. rangi* Early *et al.* 2001) was collected from North Island forest by S. & J. Peck of Ottawa in 1978, the single female specimen also finding its way to LM. As interest in the New Zealand hymenopteran fauna and the use of specialist collecting techniques developed during the 1980s, in particular the use of screen sweeping and yellow pan trapping, so did the number of specimens, until now when both species are known to be abundant and sufficient material was available for dissection, scanning electron microscopy and molecular analysis. The family Maamingidae, comprising these two species in the new genus *Maaminga*, was formally established by Early *et al.* (2001), this paper being in press at the time of the symposium.

Information on the Maamingidae has been published previously in several papers dealing with the fauna of New Zealand. It was first referred to as a “New family” and illustrated as a half-tone photograph in Grehan (1990), while Early (1995) later describes it as a “Parasitic wasp, undescribed family” (see under *M. rangi*). There are now numerous other references to “undescribed proctotrupoid family” or “undescribed New Zealand family” in recent phylogenetic studies on the Hymenoptera (e.g. Basibuyuk & Quicke 1997, 1999a, b; Dowton *et al.* 1997; Basibuyuk *et al.* 2000). Information is presented here on their distribution and apparent habitat preferences, but their host biology remains unknown. The superfamily placement and possible relationships of Maamingidae to other proctotrupoid families are discussed in the light of current morphological and molecular phylogenetic hypotheses.

The species

Maaminga rangi (Fig. 1)

This species has been recorded from the North Island and northern South Island (Fig. 3) but has not been found in other parts of the South Island despite intensive collecting effort in those regions. *Maaminga rangi* lives in forest of various types (*Agathis*-podocarp-broadleaf, broadleaf-nikau palm, *Nothofagus* (southern beech), mixed *Nothofagus*-podocarp/broadleaf). It is the smaller (1.1 – 1.5 mm long) and more gracile species with large wings in proportion to body size. Despite this, it is not a strong flier and confines its activity close to the forest floor where it is particularly abundant and easily collected in pan traps and by sweeping ferns and ground cover, particularly in the *Agathis*-podocarp forests north of Auckland. It is found throughout the summer but is more common and abundant earlier in the season (December). Hosts are unknown.



Figure 1 Female *Maaminga rangi*

Maaminga marrisi (Fig. 2)

This species is known from the North and South Islands (Fig. 1) and is sympatric with *M. rangi* at one known locality (East Cape, Fig. 3). *Maaminga marrisi* is a leaf litter inhabitant of bushy

scrub in exposed sites, from near the shoreline but also in montane/subalpine shrubs and snow tussock at about 800 m.; only a few specimens have been found in forest. Coastal sites are under the strong maritime influence of wind and salt spray, and can be hot and dry in summer. Most specimens were taken from this habitat on small offshore islands in low tangled coastal scrub close to the shoreline. Such areas are also home to New Zealand's unique reptile, the tuatara (*Sphenodon punctatus* (Gray) and *S. guntheri* Buller, Reptilia: Rhynchocephalia) and nesting seabirds (various petrels and shearwaters (Procellariiformes) and penguins (Sphenisciformes)). The higher altitude sites are all well inland but are exposed to strong winds, hot dry summers and periodic winter snow cover. The two types of habitat (coastal/maritime and montane/subalpine) invite speculation that this species may be a composite of two cryptic species.



Figure 2 Female *Maaminga marrisi*

Specimens are best collected using yellow pan traps, pitfall traps and Berlese extraction. Hosts are unknown, possibly Phoridae (Diptera) which abound in the same habitat on the small offshore islands.

This species is slightly larger (females 1.6–1.8 mm long) and more stocky than *M. rangi*. It displays plasticity in wing length, although the distinction between brachypterous and macropterous morphs is arbitrary. While it is clear at the extremes of the range, the ratio of wing to body length is a continuum from 0.6–1.3. All specimens from the most northern recorded localities are macropterous while the majority from more southern localities are predominantly brachypterous. Reduced wings and long hind legs are common among New Zealand proctotrupoid and platygastroid wasps and indicate adaptations to inhabiting leaf litter (Austin 1988; Early, *unpubl.*; Naumann 1988).

Family placement and phylogenetic relationships

Family level status of Maamingidae

The two recorded species of *Maaminga* represent a unique combination of characters. In particular, the form of the head, antennae, some features of the mesosoma, and wings resemble members of the Diapriidae (and possibly the Monomachidae). On the other hand, the metasoma, subgenital plate and external ovipositor are reminiscent of the Ichneumonoidea. Nominally, Maamingidae and Diapriidae can be allied on the basis of two putative synapomorphies, the antennae inserted onto a prominent frontal shelf, and the presence of obvious curved trichoid sensilla on the antennae. However, the presence of a facial shelf may be a synapomorphy for Diapriidae + Maamingidae + Monomachidae, although in the latter family this character is not as obvious and it may be homoplasious given that a frontal shelf is also known to occur in other groups of Hymenoptera, e.g. orthocentrine ichneumonids and Embolemyidae. One proposition is to recognise *Maaminga* as a subfamily of Diapriidae, although this would require significantly broadening of the morphological limits to this family, which is otherwise easily identified and well defined morphologically. Further, recent molecular studies do not support a direct sister group relationship between *Maaminga* and Diapriidae, and the two groups differ in several important characters as follows:

Maaminga: female:male antennal segments 13:12; male antenna without a sex segment; palpal formula 2:2; occipital carina absent; lateral pronotum striated; junction between lateral pronotum and mesopleuron membranous and flexible; metasoma unspecialised, T3 and S3 not enlarged.

Diapriidae: female:male antennal segment number variable, never 13:12; male antenna often with a sex segment; palpal formula 5:3; occipital carina present; lateral pronotum not striated; suture between lateral pronotum and mesopleuron rigid; T3 and S3 enlarged.

In summary, although the currently available data are not particularly robust, there are reasonable grounds to place *Maaminga* in a new family separate to the Diapriidae, until the relationships of the proctotrupoid complex are better resolved.

Superfamily placement

Maaminga is excluded from all apocritan superfamilies (except the Proctotrupeoidea *s. str.*) on the following grounds:

- 1 Insertion of metasoma low on the petiole between the hind coxae (excluded from Evanioidea).
- 2 Absence of vein C in fore wing, hence costal cell is open (excluded from Evanioidea, Stephanoidea, Trigonoidea, Megalyroidea, Ichneumonoidea, Chrysidoidea (except Chrysididae: Lobescelidiinae), Vespoidea, Apoidea).
- 3 Only one foretibial spur, presence of open costal cell, absence of syntergite, presence of metasomal spiracle (excluded from Ceraphronoidea).
- 4 Absence of placoid sensilla on antennae (excluded from Ichneumonoidea, Cynipoidea, Chalcidoidea).

- 5 Single segment to petiole, head without bellows-like structure, wings not reticulate (excluded from Mymarommatoidea)
- 6 Ovipositor not detached from terminal metasomal segments and not retracted internally within a desclerotised tubular part of abdominal segment 9 (excluded from Platygastroidea)

Given the apparent similarity of *Maaminga* to Diapriidae, the Proctotrupoidea is then the only likely candidate for the superfamily placement of the genus. However, there are no characters that unite this superfamily and, as indicated above, the placement of Maamingidae in this group is based more on the absence of synapomorphies that define the other superfamilies of Apocrita. Further, there is now mounting evidence that the Proctotrupoidea as recognised by previous authors (e.g. Naumann & Masner 1985; Masner 1993, 1995; Gauld & Bolton 1996) is polyphyletic.

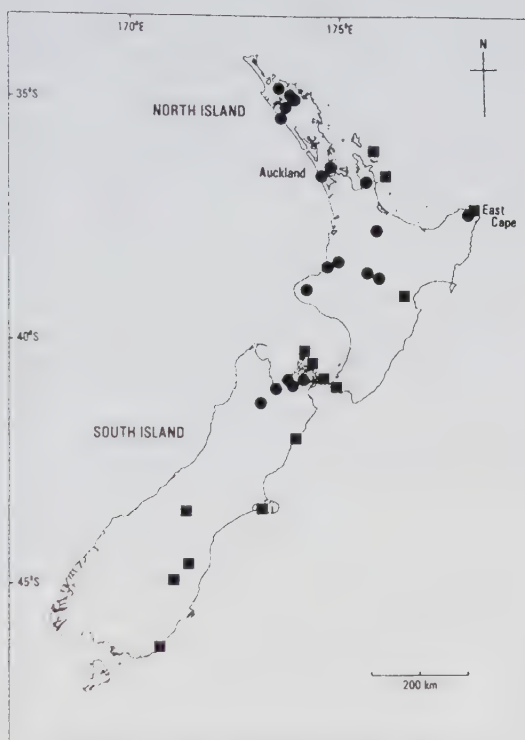


Figure 3 Distribution of *M. rangi* (circles) and *M. marrisi* (squares) in New Zealand

Family relationships within the Proctotrupomorpha *sensu* Rasnitsyn (1988) are the subject of several recent studies (see references in Early *et al.* 2001 for a fuller discussion) and are ongoing. The inevitable question arises: Where does Maamingidae sit in relation to other proctotrupoid families? The most recent hypothesis, based on molecular evidence from three genes (nuclear 28S rDNA, cytochrome oxidase I and mitochondrial 16S rDNA) comes from Dowton & Austin (*in press*) in an extensive study aimed at trying to resolve family relationships within the parasitic

wasps. Their analyses recovered the Maamingidae generally as the sister group to the Monomachidae, with this clade being the sister group to the Diapriidae. Although the monophyly of these three families is relatively stable, their precise position relative to each other is not, with some analyses (Dowton & Austin, *in press*) placing the Maamingidae as the sister group to the Monomachidae + Diapriidae. Clearly, the last word has not yet been spoken and the phylogeny of the Proctotrupeoidea still awaits resolution.

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WESTERN PALAEARCTIC GENERA OF THE SUBFAMILY MICROGASTRINAE: A RE-APPRAISAL OF THE GENERIC AND TRIBAL DIVISION (HYMENOPTERA: BRACONIDAE)

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Abstract — The generic division of the subfamily Microgastrinae is discussed and suggestions are made how to improve the division, both from a practical as well as from a phylogenetical viewpoint. The suggested division is compared with existing divisions and the fit with biological and DNA data is discussed. In total 48 new combinations of specific names in the European Microgastrinae are proposed and a list of European Microgastrinae is added.

Key words: Hymenoptera, Microgastrinae, *Apanteles*, Western Palaearctic, Europe, generic division, tribes

Introduction

The subfamily Microgastrinae Foerster, 1862, is the most commonly collected subfamily and one of the largest subfamilies of the family Braconidae (Hymenoptera), it may contain up to 10 000 species (Mason 1981) or more. The generic division most often used presently is by Mason (1981) poses practical problems because of lack of well defined character-states for several genera, and of overlap between supposedly not closely related genera. For instance, Tobias (1986, 1995): “It is difficult to separate most *Apanteles* groups (especially such large groups as *A. glomerata*, *A. popularis*, etc.) from each other due to the large number of intermediate species, which can only conditionally be included in one of the groups.” In addition, there are doubts about the phylogenetical value of part of the grouping, the absence of a character-matrix does not allow checking of characters and about the method used for the phylogenetical analysis (Austin 1990). In Mason’s (1981) analysis 13 out of the 34 characters concern autoapomorphies and are uninformative about relationships, several important characters are homoplasous on the (hand-generated) phylogenetic tree, several clades (including the tribe Apantelini) are not defined by any synapomorphous character-state, several characters are wrongly polarised, genera are grouped in *a priori* groups and an *a priori* linking of character-states occurs in the “macrolepidoptera suite”.

A recent 16SrDNA, 28SrDNA and COI analysis by Mardulyn & Whitfield (1999) also raises doubts about the validity of the system. Mardulyn & Whitfield (1999; the latter being one of the advocates of the system proposed by Mason (1981)), conclude that there is a lack of signal among the nearly 2300 nucleotides examined (summary of results in Fig. 4). However, they suggest that this “is an indication of the presence of many short internal branches on the phylogeny estimated, which in turn might be the result of a rapid diversification of the taxa examined”. A peculiar conclusion considering the weakness of the underlying taxonomic system; would it not be wiser to have a closer look at this system before hand?

Currently two generic divisions are used: a) the proposed system by Mason (1981: 50 extant genera in 5 tribes, with addition of some new taxa (Williams 1985; Austin & Dangerfield 1992; Whitfield 1997; summarised in Fig. 3a); and b) the division in species-groups of the genus *Apanteles* Foerster, 1862 s.l. by Nixon (1965, 1973), resulting in 19 genera and one tribe. Tobias (1986) follows mostly Nixon's system for *Apanteles* s.l., and Mason's system for the other groups; van Achterberg (1997) applied an intermediary generic division in the catalogue of the taxa described by A.H. Haliday. Papp (1976-1990) for his revision of the Western Palaearctic species of *Apanteles* s.l. applied first the system of species groups of Nixon with some groups modified, but later (Papp 1988) regrouped the Palaearctic species according to the species-lists given by Mason (1981). No key to the Palaearctic genera was given by Papp (1988), but because Mason's proposal is based on re-grouping of existing species-groups, Papp's key to the species-groups could be used. This last key (as the following ones on the species-groups themselves) illustrates well partly the problem: even the species-groups can not be defined unambiguously and show overlap or similarity with species-groups partly assumed to belong to (more or less related) different genera according to Mason's system. For instance, Papp (1981) gives for the 16 species in the *Apanteles ultor* group 4 intermediate species belonging to the *A. ater* and *A. obscurus* groups. The first belongs to *Dolichogenidea* Viereck, 1911, and both last groups to *Apanteles* Foerster, 1862, according to Mason's system. In the same paper, the 18 species of the *A. butalidis* group (= *Illidops* Mason, 1981) have 3 intermediate species belonging to the genera *Illidops*, *Dolichogenidea* and *Apanteles* according to Mason's proposal. Difficulties to assign males to a certain genus is another indication of incorrect grouping concepts, including over splitting.

Mason (1981) proposed his generic division in the spirit of no more than a first hypothesis (*pers. comm.*) as several important assumptions seem questionable and many relationships are still unclear. "However, Mason's classification has been widely adopted by applied biologists, and it is rather unfortunate that such a large number of generic names are being taken up so enthusiastically in advance of further critical analysis of the group by systematists, which remains a clear need" (Shaw & Huddleston 1991). We are 10 years further and the situation is not improved, on the contrary, also systematists apply the genera more and more (e.g. Papp 1988; Whitfield 1997; Austin & Dangerfield 1992), despite the well-founded and extensive criticism by Austin (1990).

What may have gone wrong?

Only two re-appraisals of Mason's paper have been undertaken: Walker *et al.* (1990) reassessed the phylogenetical analysis according to modern standards. The result was a hardly informative, largely polytomous consensus tree of 185–512 equally parsimonious trees! Their conclusion was that Mason (1981) correctly assumed that the absence of the vein r-m in fore wing is a subject to considerable homoplasy. This could be expected because it is a negative (= reductive) character-state. Two groups could be separated, but only on their biology and the suite of correlated characters. One group with longer ovipositors and parasitising more concealed hosts ("microleps"). The other group has short ovipositors and contains parasitoids of exposed hosts ("macroleps" or the macrolepidoptera character suite of Mason (1981)). They hinted that the system of using groups of genera (in Mason's sense) in the phylogenetical analysis may be not justified. Unfortunately, they used the same system for their analysis.

Maetô (1996) examined extensively the male genitalia of Microgastrinae to reassess Mason's tribal division. One main clade contains the genus *Apanteles* s.m., *Microgaster* and *Hygroplitis*, i.e. it concerns the end of the tree as given in this paper and the recognition of a separate tribe Apantelini is unsupported. The remainder of the Microgastrinae is supposed to be supported by three synapomorphies (Maetô 1996). The absence of the ectoparasitic phase (which is related to the biology; an ectoparasitic phase on an exposed host is biologically speaking suicidal!), the sculpture of the scutellum medio-posteriorly (the majority of the species of the group does not have it and if present it may be not homologous in all cases) and females of four genera have derived ventral sensory fields on the antennae medially and subapically. In my opinion the evidence for monophyly is too weak and the characters used are too variable to be used in this way.



Figure 1 *Protapanteles* sp. from podborer on *Cajanus cajan* (Linnaeus) in Malawi
(by Polaszek, A. & Kibby, G.)

Essential for a better understanding is to leave this tactic and to have a fresh look at the (supposed) genera independently as is tried in this study. Secondly, Mason used as main character for grouping the relative length of the ovipositor and its sheath (including the setosity of the latter). Not so surprisingly this proved to fit in with the biology of the supposed genera-groups, because this is a direct causal relation (Tobias 1986). Only the biology or the relative length of the ovipositor (and without direct correlated characters) should have been used as arguments but not both, because it concerns the same adaptation from a biological point of view and the whole suite will obscure the underlying relationships. In this study the biology is not used *a priori*, but the length of the ovipositor sheath in combination with the sclerotisation of the hypopygium. All supposed genera available are checked for a set of characters supposed to be not direct causally

related to each other. No data-matrix is given because of the preliminary nature of the analysis, but from Austin (1990) and Walker *et al.* (1990) nearly most data can be distracted. The grouping of most species-groups into genera I found untenable, as several of the *a priori* groupings. For instance, grouping of the genus *Cotesia* Cameron, 1891 with genera *Protopanteles* Ashmead, 1898 and *Glyptapanteles* Asmead, 1905 by Mason (1981), I consider to be a misfit. This at least partially explains the observed problems of the proposed generic division of *Apanteles* s.l., together with the weight given to Mason's "macroplepidoptera suite" of characters.

A fresh look?

For this study a set of characters assumed to be not direct causally related to each other (Table 1) have been used to examine proximally 120 mainly Western Palaearctic species of *Apanteles*

Table 1 Characters used for analysis of the Western Palaearctic genera (see van Achterberg (1988) for the technical terms; T1, T2, and T3 refer to the first, second and third metasomal tergites, respectively)

Plesiomorphous character-state	Apomorphous character-state
1. Ovipositor sheath slender and short	long and more or less widened ("falcate")
2. Scutellar sulcus wide and strongly crenulate	narrow or obsolescent, hardly crenulated
3. Submedial area of metanotum straight anteriorly and no posterior elongate depression	more or less concave anteriorly or shallowly depressed and elongate depression present
4. Propodeum wing short median carina and posterior areola	median carina complete or lost or coarsely reticulate
5. Vein 1-SR of fore wing not angled with vein 1-M pointed to vein 1-CU1	angled, pointed to vein 2-CU1
6. Fore telotarsus without straight or curved spur	spur present
7. Vein 1-CU1 of fore wing about same level as 2-CU1 and subhorizontal	vein 1-CU1 higher than 2-CU1 and strongly oblique
8. T1 without sharp medial groove	median groove at least basally present
9. Apical antennal segments slender	apical antennal segments moniliform
10. Vein 2-M of fore wing comparatively short, about as long as vein 2-SR	vein 2-M reduced
11. Hind coxae small, reaching up to apex of T1	enlarged, reaching T3, usually to its apex
12. Hypopygium of female sclerotised	folded, partly desclerotised
13. T1 wide and apically robust	narrow(ed) and apically slender
14. T2 about as long as T3 or somewhat shorter	T2 about half as long as T3
15. T2 with long medial area or area absent	medial area short, small
16. Lateral grooves of T1 (as far as present) sublateral	grooves submedial
17. Vein 1-SR of fore wing medium-sized and slender	short and/or widened
18. Vein cu-a of hind wing straight and vertically	reclivous and more or less sinuate
19. Vein r-m of fore wing present	absent
20. Vein 1-CU1 of fore wing short	long
21. Propodeum medium-sized medio-dorsally	short medio-dorsally
22. Precoxal sulcus present	absent

Foerster s.l. and the other genera were examined afterwards. From the beginning it has been clear that most characters are showing overlap between Mason's genera, and the main strategy has been to re-group the species-groups to minimise the overlap, and consequently, lower the number of recognised genera.

Outgroup and plesiomorphous character-states

What is the base-plan of the group, or what are the supposed plesiomorphous character-states? What is the outgroup? Generally (e.g. Quicke & van Achterberg 1990; Belshaw *et al.* 1999) the Cardiochilinae and Khoikhoiinae are considered to form together the sister-group of the Microgastrinae, with the Miracinae as the sister-group of the three subfamilies. The prepectal carina is absent in Cardiochilinae and Khoikhoiinae (but sometimes present in the Microgastrinae) and the hind coxa is also comparatively large in both subfamilies (and in Cardiochilinae also the medially desclerotised hypopygium occurs). Most likely in the Microgastrinae still less derived character-states occur (e.g., small hind coxa, presence of prepectal carina), which are already lost in the Cardiochilinae and Khoikhoiinae. Also according to molecular studies by Mardulyn & Whitfield (1999; only 16SrDNA results, Fig. 4) and Belshaw *et al.* (1999) it seems best to use Miracinae as out-group (as the most directly basal group to the branching off of the Microgastrinae and Cardiochilinae (including Khoikhoiinae)).

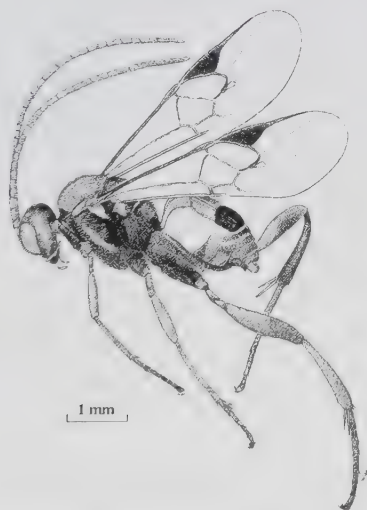


Figure 2 *Diolcogaster* sp. from Zimbabwe (by Watsham, A.)

The polarity of the sclerotisation of the female hypopygium was wrongly assigned by Mason (1981). What may have confused him is that the desclerotisation of the hypopygium has been independently evolved within two subfamilies, the Cardiochilinae and Microgastrinae, although it is slightly different in structure in each case (Austin 1990).

Provisional results

According to Mason (1981) the West Palaearctic members of the genus *Apanteles* s.l. should be divided among 12 genera. According to my provisional analysis (Fig. 5) four genera will do at least as well (and in addition some of the synonymised genera are used as subgenera). The most basal group is formed by the Microplitini with small hind coxa, and more or less developed precoxal sulcus (including *Paroplitis*), and containing parasitoids of more or less on exposed living lepidopterous larvae. The remainder of the subfamily (the Microgastrini) has enlarged hind coxa and reduced maxillary palp. Next comes an intermediary group also on exposed living lepidopterous larvae and containing the genus *Cotesia* with reticulate propodeum, vein 1-SR of fore wing pointed to vein1-CU1 and the scutellar sulcus in general more developed than in other Microgastrinae.

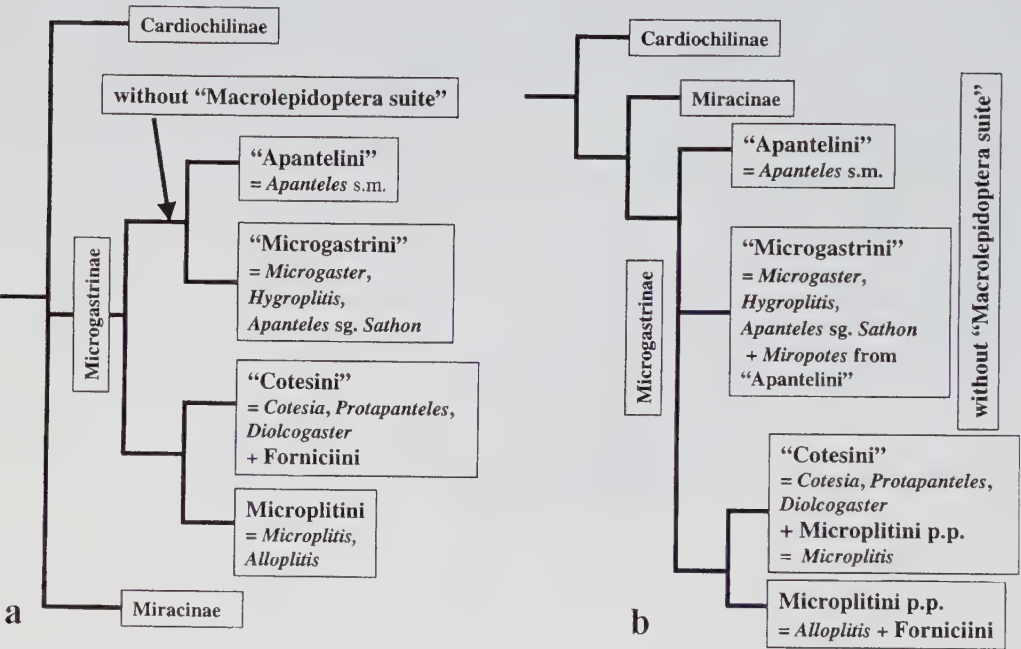


Figure 3 a, Summary of Mason's (1981) phylogenetic tree of the subfamily Microgastrinae; b, Summary of the strict consensus tree resulting from the reassessment of Mason's (1981) data by Walker et al. (1990)

Remain the Microgastrinae with modified first discal cell of fore wing and consisting of two major groups. One (= *Protapanteles* s.l.; Fig. 1) with the pair of grooves of the second metasomal tergite submedially situated, the submedial area of the metanotum straight anteriorly, the ovipositor sheath usually short, the hypopygium of female evenly sclerotised, with larvae of type II (with at most indistinct submedial dorsal teeth on mandible as in *Cotesia*; Short 1953), and containing

parasitoids of exposed lepidopterous larvae. The other group (= *Apanteles* s.l., *Microgaster* and *Hygroplitis*) has the grooves of the second tergite sublateral or obsolescent, the submedial area of metanotum more or less concave anteriorly, the ovipositor sheath usually medium-sized to long, the hypopygium of female partly unsclerotised, larvae of type I (with fine submedial teeth dorsally on mandible; Short 1953) and contains parasitoids of concealed living lepidopterous larvae. One reason this pattern was not recovered by Mason (and subsequent followers) was the practice to unite before (!) the analysis the genera in groups (Table 5 in Walker *et al.* 1990; e.g., *Protopanteles* s.l. was partly inclosed in his "Cotesiini" without clear autapomorphies). As pointed out by Maetõ (1996) several of these groups are polyphyletic if used in the sense of Mason (1981). Remain to be placed the genera *Diolcogaster* Ashmead, 1900 (parasitoids more or less exposed "macrolepidopterous" larvae; Fig. 2) and *Deuterixys* Mason, 1981 (with aberrant biology on Lyonetidae). It concerns a group of species with longitudinally grooved first metasomal tergite and often with parallel grooves submedially on the second tergite. The position of both taxa on the tree remains uncertain; the molecular data of 16SrDNA point towards a position near *Apanteles* (Mardulyn & Whitfield 1999).

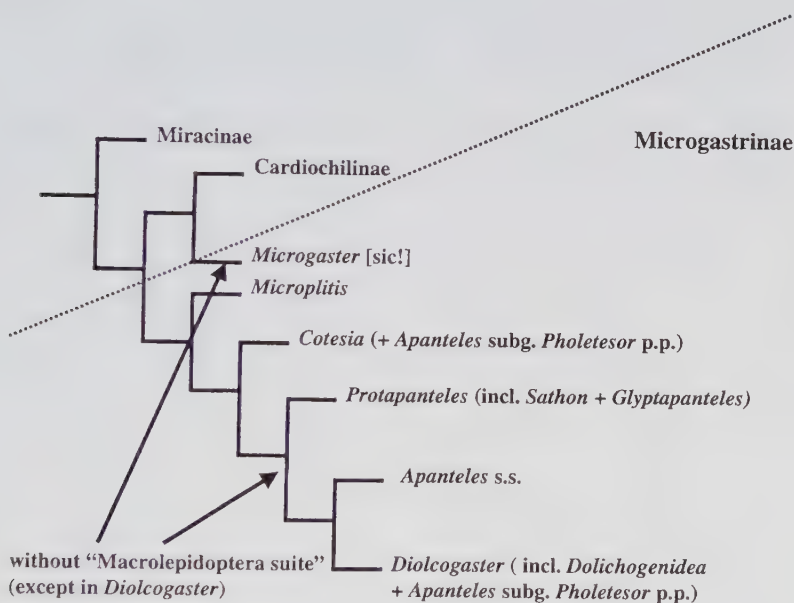


Figure 4 Summary of the 16S phylogenetic tree by Mardulyn & Whitfield (1999)

One of the surprising results of this analysis is that the presence of fine submedial dorsal teeth on the larval mandible in the Microgastrinae seems to be a derived state within the subfamily as far as the scanty biological data allow a conclusion (Figs 8–14). It may be argued that these dorsal teeth also occur in the sister groups, but the shape of the mandible is different (Figs 6–7), and the presence or absence of these teeth seems to be related to the biology. The larval mandible of *Microplitis* Foerster lacks the fine submedial dorsal teeth (Figs 8–9) and the larva emerges from an

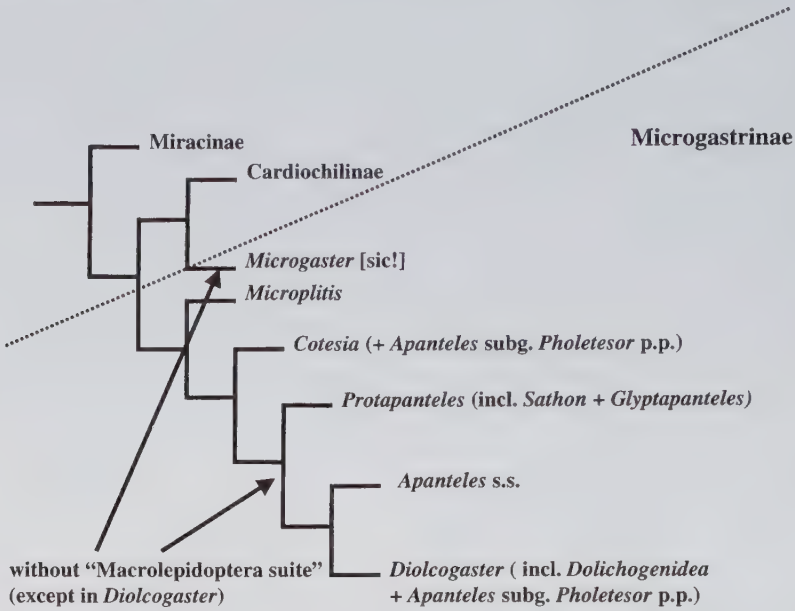
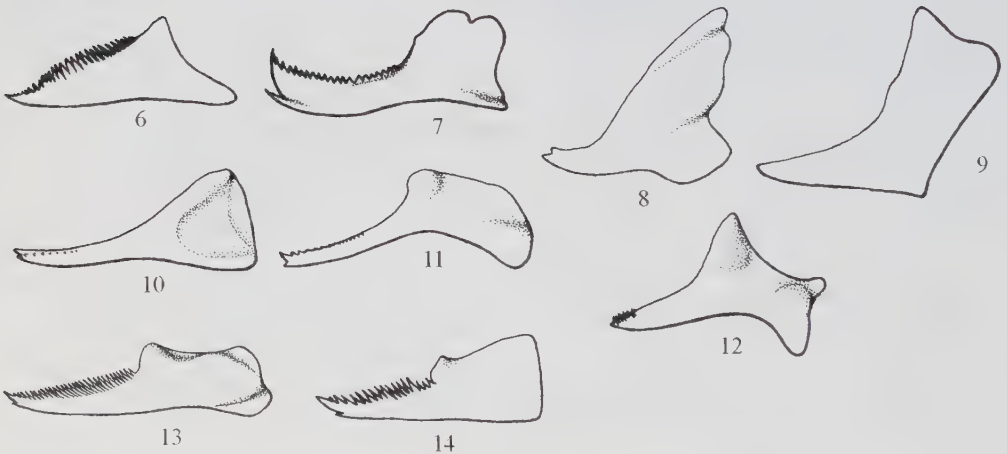


Figure 5 Summary of the results of the provisional analysis in this paper



Figures 6–14 Mandible of final instar larva: 6, Cheloninae, *Phanerotoma tibialis* (Haldeman) (after Finlayson 1967); 7, Cardiochilinae, *Cardiochiles nigriceps* Viereck (Lewis & Vinson 1968); 8–14, Microgastrinae: 8, *Microplitis mediator* (Haliday) (Arthur & Mason 1986); 9, *M. croceipes* (Cresson) (Lewis 1970); 10, *Cotesia brachycerus* (Thomson); 11, *C. melanoscela* (Ratzeburg); 12, *Protapanteles triangulator* (Wesmael) (Short 1953); 13, *Microgaster rufipes* (Nees) (Goidanich 1931); 14, *Apanteles* sp. (Finlayson 1967)

exposed host and consequently, the ectoparasitic phase (for which the toothed mandibles are used) is missing. As remarked by Shaw & Huddleston (1991) *Microgaster* selects of Nymphalidae and Hesperidae only those species whose larvae make suitable retreats in which the final ectoparasitic development of the parasitoid can take place and the mandible has submedial teeth (Fig. 13). The Cardiochilinae have a final ectoparasitic phase (Huddleston & Walker 1988, also witnessed by the presence of submedial teeth; Fig. 7), which is possible because the parasitoid emerges when the host is concealed. This allows the parasitoid to feed externally without high risk of predation.

The Microplitini have the larval mandible strongly widened basally and the blade distinctly smaller than the base (Figs 8-9). Part of *Cotesia* and *Protapanteles*, *Microgaster* and *Apanteles* have a submedial dorsal tubercle on the mandible and the base of the mandible still comparatively large, but more transverse than in the Microplitini (Figs 11-14). In *Cotesia* and *Protapanteles* the blade is more elongate and more or less narrowed (Figs 10-12) and in *Microgaster* and *Apanteles* the base of the mandible is comparatively transverse (Figs 13-14).

Table 2 The generic identity of the European species (excluding Ciscaucasus and Caucasus) of the subfamily Microgastrinae according to the conclusions in this paper. Valid species names after Papp (1988), Tobias (1986) and van Achterberg (1997). An asterisk indicates a new combination

***Apanteles* Foerster, 1862**

A. adjunctus (Nees, 1834)
A. aeolus Nixon, 1965
A. agilla Nixon, 1972
A. albinervis Tobias, 1964
A. albipennis (Nees, 1834)
A. alutaceus Balevski, 1980
A. anarsiae (Faure & Alabouvette, 1924)
A. annularis (Haliday, 1834)
A. appellator Telenga, 1949
A. aptus Papp, 1977
A. aragatzi Tobias, 1976
A. arene Nixon, 1973
A. argante Nixon, 1976
A. arisba Nixon, 1973
A. artissimus Papp, 1971
A. ate Nixon, 1973
A. atreus Nixon, 1973
A. azovicus Kutenko, 1986
A. bajariae Papp, 1975
A. barcinonensis Marshall, 1898
A. benevolens Papp, 1973
A. benkevitschi Kutenko, 1986
A. bicolor (Nees, 1834)
A. biroicus Papp, 1973
A. borysthenicus Kutenko, 1986
A. bres Nixon, 1973

A. brevivalvatus Balevski & Tobias, 1980
A. breviventrtris (Ratzeburg, 1848)
A. britannicus Wilkinson, 1941
A. brunnistigma Abdinbekova, 1969
A. butalidis Marshall, 1888
A. buteonis Kutenko, 1986
A. candidatus (Haliday, 1834)
A. carpatus (Say, 1836)
A. celsus Papp, 1975
A. cerialis Nixon, 1976
A. cheles Nixon, 1972
A. chrysis Nixon, 1973
A. cinerosus Papp, 1971
A. circumscriptus (Nees, 1834)
A. cloelia Nixon, 1965
A. colchicus Tobias, 1986
A. coleophorae Wilkinson, 1934
A. contaminatus (Haliday, 1834)
A. corvinus Reinhard, 1880
A. credne Nixon, 1973
A. cytherea Nixon, 1972
A. decorus (Haliday, 1834)
A. dilectus (Haliday, 1834)
A. dorsalis (Spinola, 1808)
A. drusilla Nixon, 1972
A. eleagnellae Tobias, 1976
A. electilis Tobias, 1964

- A. elpis* Nixon, 1973
A. emarginatus (Nees, 1834)
A. ensiformis (Ratzeburg, 1844)
A. erasmi Nixon, 1972
A. erdoesi Papp, 1973
A. erevanicus Tobias, 1976
A. errans Nixon, 1973
A. eugeni Papp, 1972
A. evanidus Papp, 1975
A. evonymellae (Bouché, 1834)
A. exilis (Haliday, 1834)
A. faucula Nixon, 1972
A. flavostriatus Papp, 1977
A. frustratus Papp, 1977
A. furtim Papp, 1977
A. gagates (Nees, 1834)
A. galleriae Wilkinson, 1932
A. gallicolus (Giraud, 1869)
A. glaber Papp, 1978
A. gnarus Tobias & Kotenko, 1984
A. gracilariae Wilkinson, 1940
A. gratus Kotenko, 1986
A. halidayi Marshall, 1872
A. helleni Nixon, 1972
A. hemerobiellcida Fischer, 1966
A. hilaris (Haliday, 1834)
A. horaeus Kotenko, 1986
A. immissus Papp, 1977
A. imperator Wilkinson, 1939
A. impurus (Nees, 1834)
A. infimus (Haliday, 1834)
A. intermedius Balevski, 1980
A. interpolatus Papp, 1975
A. isus Nixon, 1965
A. jaroshevskiyi Tobias, 1976
A. kostylevi Kotenko, 1986
A. kubensis Abdinbekova, 1969
A. lacteus (Nees, 1834)
A. lacteicolor Viereck, 1911
A. lacteipennis (Curtis, 1830)
A. lacteoides Nixon, 1965
A. laetus Marshall, 1885
A. laspeyresiellus Papp, 1972
A. laevigatus (Ratzeburg, 1848)
A. laevigatoides Nixon, 1972
A. laevisissimus (Ratzeburg, 1848)
A. lectus Tobias, 1964
A. lemariei Nixon, 1961
A. lenea Nixon, 1976
A. lineipes (Wesmael, 1837)
A. litae Nixon, 1972
A. longicalcar Thomson, 1895
A. longipalpis (Reinhard, 1880)
A. luctificus Papp, 1971
A. marica Nixon, 1972
A. maritimus Wilkinson, 1941
A. meratus Kotenko, 1981
A. metacarpalis Thomson, 1895
A. merula Reinhard, 1880
A. meruloides Nixon, 1965
A. midas Nixon, 1972
A. mimi Papp, 1974
A. miramis Nixon, 1976
A. mirus Papp, 1977
A. moldavicus Tobias, 1975
A. murinanae Čapek & Zwölfer, 1957
A. mutabilis Telenga, 1955
A. mycale Nixon, 1972
A. myeloenta Wilkinson, 1937
A. myron Nixon, 1973
A. nagyai Papp, 1975
A. nanus Reinhard, 1880
A. naso Marshall, 1885
A. nephus Papp, 1974
A. nixosiris Papp, 1976
A. obscurus (Nees, 1834)
A. obstans Papp, 1971
A. oehlkei Papp, 1982
A. pallidalatus Tobias, 1964
A. parasitellae (Bouché, 1834)
A. pelopea Nixon, 1973
A. peridoneus Papp, 1974
A. petrovae Walley, 1937
A. phaetusa Nixon, 1973
A. phaloniae Wilkinson, 1940
A. phaola Nixon, 1972
A. planiscapus Tobias, 1976
A. piliventris Tobias, 1966
A. praetor Marshall, 1885
A. princeps Wilkinson, 1941
A. probatus Papp, 1973
A. propinquus Papp, 1975
A. punctiger (Wesmael, 1837)
A. purdus Papp, 1977
A. reicharti Papp, 1974
A. rostratus Tobias, 1976
A. ruficornis (Nees, 1834)
A. rufulus Tobias, 1964

- A. salalicus* Mason, 1959
A. scutellaris Muesebeck, 1921
A. seriphia Nixon, 1972
A. sicarius Marshall, 1885
A. sisenna Nixon, 1972
A. sodalis (Haliday, 1834)
A. soikai (Nixon, 1972)
A. sophiae Papp, 1972
A. sophrosine Nixon, 1976
A. splendidus Papp, 1974
A. submarginatus Abdinbekova, 1969
A. suevus Reinhard, 1880
A. suffolciensis (Morley, 1902)
A. szaboi Papp, 1972
A. szalayi Papp, 1977
A. szelenyii Papp, 1972
A. tedellae Nixon, 1961
A. tiro Reinhard, 1880
A. tobiasi Balevski, 1980
A. trachalus Nixon, 1965
A. turionellae Nixon, 1971
A. ultimus Kotenko, 1986
A. ultor Reinhard, 1880
A. urgo Nixon, 1965
A. validus Thomson, 1895
A. victor Wilkinson, 1941
A. victoriatu Kotenko, 1986
A. viminetorum (Wesmael, 1837)
A. vindicia Nixon, 1965
A. vipio Reinhard, 1880
A. xanthostigma (Haliday, 1834)
- Cotesia** Cameron, 1891
C. abjecta (Marshall, 1885)
C. acuminata (Reinhard, 1880)
C. acutula (Tobias, 1973)
C. affinis (Nees, 1834)
C. amesis (Nixon, 1974)
C. analis (Nees, 1834)
C. ancilla (Nixon, 1974)
C. arctica (Thomson, 1895)
C. aurura (Telenga, 1955)
C. berberis (Nixon, 1974)
C. bignellii (Marshall, 1885)
C. brachycera (Thomson, 1895)
C. brevicornis (Wesmael, 1837)
C. cajae (Bouché, 1834)
C. calimone (Nixon, 1974)
C. calodetta (Nixon, 1974)
C. capucinae (Fischer, 1961)
C. chares (Nixon, 1865)
C. cleora (Nixon, 1974)
C. clepta (Tobias, 1986)
C. corylicola (Tobias, 1986)
C. cultellata (Tobias, 1966)
C. cuprea (Lyle, 1925)
C. cynthiae (Nixon, 1974)
C. depressithorax (Tobias, 1964)
C. disparis (Tobias, 1986)
C. errator (Nixon, 1974)
C. eulipis (Nixon, 1974)
C. euryale (Nixon, 1974)
C. evagata (Papp, 1973)
C. ferruginea (Marshall, 1885)
C. flagitata (Papp, 1971)
C. fluvialis (Balevski, 1980)
C. gades (Nixon, 1974)
C. gastropachae (Bouché, 1834)
C. geryonis (Marshall, 1885)
C. glabrata (Telenga, 1955)
C. glomerata (Linnaeus, 1758)
C. gonopterygis (Marshall, 1898)
C. hyphantriae (Riley, 1887)
C. inducta (Papp, 1973)
C. intermixta (Balevski, 1980)
C. isolde (Nixon, 1974)
C. jucunda (Marshall, 1885)
C. judaica (Papp, 1970)
C. juniperatae (Bouché, 1834)
C. kazak (Telenga, 1949)
C. kurdjumovi (Telenga, 1955)
C. limbata (Marshall, 1885)
C. lineola (Curtis, 1830)
C. lycophron (Nixon, 1974)
C. melanoscela (Ratzeburg, 1844)
C. mendicae (Tobias, 1986)
C. memnon (Nixon, 1974)
C. microsoma (Tobias, 1986)
C. neustriae (Tobias, 1986)
C. nigrithibialis (Tobias, 1986)
C. nothus (Marshall, 1885)
C. numen (Nixon, 1974)
C. ocnariae (Ivanov, 1898)
C. ofella (Nixon, 1974)
C. onaspis (Nixon, 1974)
C. ordinaria (Ratzeburg, 1844)
C. orestes (Nixon, 1974)
C. peltoneni (Papp, 1987)

C. pieridis (Bouché, 1834)
C. pilicornis (Thomson, 1895)
C. plutellae (Kurdjumov, 1912)
C. praepotens (Haliday, 1834)
C. risilis (Nixon, 1974)
C. rubecula (Marshall, 1885)
C. rubripes (Haliday, 1834)
C. ruficrus (Haliday, 1834)
C. ruficentris (Abdinbekova, 1969)
C. salebrosa (Marshall, 1885)
C. saltator (Thunberg, 1822)
C. saltatoria (Balevski, 1980)
C. satunini (Tobias, 1986)
C. scabricula (Reinhard, 1880)
C. scelerata (Tobias, 1986)
C. setebis (Nixon, 1974)
C. shemachaensis (Tobias, 1976)
C. sibyllarum (Wilkinson, 1936)
C. specularis (Szépligeti, 1896)
C. spuria (Wesmael, 1837)
C. subancilla (Balevski, 1980)
C. subordinaria (Tobias, 1972)
C. telengai (Tobias, 1972)
C. tenebrosa (Wesmael, 1837)
C. tetrica (Reinhard, 1880)
C. tibialis (Curtis, 1830)
C. vanessae (Reinhard, 1880)
C. vestalis (Haliday, 1834)
C. villana (Reinhard, 1880)
C. viridanae (Tobias, 1986)
C. zygaenarum (Marshall, 1885)

Deuterixys Mason, 1981

D. carbonaria (Wesmael, 1837)
D. condarensis (Tobias, 1960)
D. plugarui (Tobias, 1975)
D. rimulosa (Niezabitowski, 1910)

Diolcogaster Ashmead, 1898

D. abdominalis (Nees, 1834)
D. alvearia (Fabricius, 1798)
D. claritibia (Papp, 1959)
D. connexa (Nees, 1834)
D. flavipes (Haliday, 1834)
D. hinzi (Nixon, 1965)
D. mayae (Shestakov, 1932)
D. meges (Nixon, 1965)
D. minuta (Reinhard, 1880)

D. procris (Fischer, 1964)
D. rufula Papp, 1990
D. scotica (Marshall, 1885)
D. spreta (Marshall, 1885)

Hygroplitis Thomson, 1895

H. pseudorussatus Shaw, 1992
H. rugulosus (Nees, 1834)
H. russatus (Haliday, 1834)

Microgaster Latreille, 1804

M. acilia Nixon, 1968
M. alebion Nixon, 1968
M. areolaris Thomson, 1895
M. asramenes Nixon, 1968
M. auriculata (Fabricius, 1804)
M. australis Thomson, 1895)
M. campestris Tobias, 1964
M. caris Nixon, 1968
M. chrysosternis (Tobias, 1986)
M. consors Nixon, 1968
M. crassicornis Ruthe, 1860
M. deceptor Nixon, 1968
M. deductor Nixon, 1968
M. ductilis Nixon, 1968
M. dudichi Papp, 1961
M. erro Nixon, 1968
M. eupolis Nixon, 1968
M. fischeri Papp, 1960
M. famula Nixon, 1968
M. fulvicrus Thomson, 1895
M. fusca Papp, 1959
M. hospes Marshall, 1885
M. hungarica Szépligeti, 1896
M. incurvata Papp, 1976
M. luctuosa Haliday, 1834
M. meridiana Haliday, 1834
M. messoria Haliday, 1834
M. nigricans Nees, 1834
M. nitidula Wesmael, 1837
M. nobilis Reinhard, 1880
M. novicia Marshall, 1885
M. opheltes Nixon, 1968
M. pantographae Muesebeck, 1922
M. parvistriga Thomson, 1895
M. polita Marshall, 1885
M. postica Nees, 1834

M. procera Ruthe, 1860
M. rufipes Nees, 1834
M. rugosicoxa Papp, 1959
M. stictica Ruthe, 1858
M. subcompleta Nees, 1834
M. subtilipunctata Papp, 1959
M. uliginosa Thomson, 1895

***Microplitis* Foerster, 1862**

M. aduncus (Ruthe, 1860)
M. ariatus Papp, 1979
M. blascoi Papp & Shaw, 2001
M. capeki Nixon, 1970
M. cebes Nixon, 1970
M. coactus Lundbeck, 1896
**M. combinatus* (Papp, 1984)
M. decens Tobias, 1964
M. decipiens (Prell, 1925)
M. deprimator (Fabricius, 1798)
M. docilis Nixon, 1970
M. eremita Reinhard, 1880
M. erythrogaster Abdinbekova, 1969
M. excisus Telenga, 1955
M. flavipalpis (Brullé, 1832)
M. fordii Nixon, 1970
M. fulvicornis (Wesmael, 1837)
M. heterocerus (Ruthe, 1860)
M. hispalensis Marshall, 1898
M. idia Nixon, 1970
M. impressus (Wesmael, 1837)
**M. improvisus* (Papp, 1984)
M. leoniae Niezabitowski, 1910
M. lugubris (Ruthe, 1860)
**M. malimbus* (Papp, 1984)
M. mandibularis (Thomson, 1895)
M. marshallii Kokujev, 1897
M. mediator (Haliday, 1834)
M. moestus (Ratzeburg, 1852)
M. naenia Nixon, 1970
M. necopinatus (Papp, 1984)
M. ocellatae (Bouché, 1834)
M. ochraceus Szépligeti, 1896
M. pallidipennis Tobias, 1964
M. pellucidus Telenga, 1955
M. pseudomurinus Abdinbekova, 1969
M. ratzeburgii (Ruthe, 1858)
**M. retentus* (Papp, 1984)
M. rufiventris Kokujev, 1914
M. scrophulariae Szépligeti, 1898

**M. serotinus* (Papp, 1984)
M. sofron Nixon, 1970
M. spectabilis (Haliday, 1834)
M. spinolae (Nees, 1834)
M. strenuus Reinhard, 1880
M. tadzhicus (Telenga, 1949)
M. testaceicornis Niezabitowski, 1910
M. tristis (Nees, 1834)
M. tuberculatus (Bouché, 1834)
M. tuberculifer (Wesmael, 1837)
M. xanthopus (Ruthe, 1860)
M. varipes (Ruthe, 1860)
M. viduus (Ruthe, 1860)

***Paroplitis* Mason, 1981**

P. wesmaeli (Ruthe, 1860)

***Protopanteles* Ashmead, 1900**

**P. acasta* (Nixon, 1973)
**P. aletta* (Nixon, 1973)
**P. aliphera* (Nixon, 1973)
P. anchisiades (Nixon, 1973)
P. andromica (Nixon, 1976)
**P. antinoe* (Nixon, 1973)
**P. calceatus* (Haliday, 1834)
**P. callidus* (Haliday, 1834)
**P. circumvectus* (Lyle, 1918)
**P. compressiventris* (Muesebeck, 1921)
P. delitutus (Papp, 1984)
**P. desueta* (Papp, 1989)
P. endemus (Nixon, 1965)
P. enephes (Nixon, 1965)
**P. eugeni* (Papp, 1972)
**P. falcatus* (Nees, 1834)
**P. fausta* (Nixon, 1973)
**P. formosus* (Wesmael, 1837)
**P. fraternus* (Reinhard, 1880)
**P. fulvipes* (Haliday, 1834)
P. hirtariae (Kotenko & Tobias, 1986)
P. iapetus (Nixon, 1976)
P. immunis (Haliday, 1834)
P. incertus (Ruthe, 1859)
**P. inclusus* (Ratzeburg, 1844)
**P. intermedius* (Balevski, 1980)
**P. iraklii* (Kotenko, 1986)
**P. karadagi* (Tobias, 1986)
**P. lateralis* (Haliday, 1834)
**P. liparidis* (Bouché, 1834)
**P. luciana* (Nixon, 1973)

- | | |
|--|---|
| * <i>P. majalis</i> (Wesmael, 1837) | * <i>P. pinicola</i> (Lyle, 1917) |
| <i>P. mandanis</i> (Nixon, 1965) | * <i>P. pompelon</i> (Nixon, 1965) |
| * <i>P. marginatus</i> (Nees, 1834) | <i>P. popularis</i> (Haliday, 1834) |
| * <i>P. menander</i> (Nixon, 1973) | * <i>P. porthetriae</i> (Muesebeck, 1928) |
| * <i>P. militaris</i> (Walsh, 1961) | * <i>P. querceus</i> (Tobias, 1986) |
| * <i>P. mygdonia</i> (Nixon, 1973) | * <i>P. ripus</i> (Papp, 1983) |
| * <i>P. nigerrimus</i> (Roman, 1924) | * <i>P. rubens</i> (Reinhard, 1880) |
| * <i>P. nivalis</i> (Papp, 1983) | * <i>P. salepus</i> (Papp, 1983) |
| * <i>P. octonarius</i> (Ratzeburg, 1852) | * <i>P. sancus</i> (Nixon, 1965) |
| * <i>P. palabundus</i> (Tobias, 1986) | * <i>P. sublateralis</i> (Tobias, 1976) |
| * <i>P. pallipes</i> (Reinhard, 1880) | * <i>P. thompsoni</i> (Lyle, 1927) |
| <i>P. parallelus</i> (Lyle, 1917) | <i>P. triangulator</i> (Wesmael, 1837) |
| * <i>P. penelopeus</i> (Tobias, 1986) | * <i>P. vitripennis</i> (Curtis, 1830) |

Conclusions

The subfamily Microgastrinae is oversplitted and for the West Palaearctic fauna about 9 genera (in stead of 18 genera: Mason 1981; Papp 1988) will suffice.

The genus *Apanteles* Foerster s.l. (Nixon 1965, 1973) is polyphyletic and should be splitted in about 4 genera; the loss (or strong reduction) of vein r-m of fore wing occurred at least 3 times independently.

The following simplified evolutionary scenario is plausible (Fig. 5):

- 1) The basal group of Microgastrinae possesses small hind coxa and contains parasitoids of "Macroleps" (Microplitini). The basal position is supported by the analysis of 16SrDNA (Mardulyn & Whitfield 1999; Fig. 4) and the combined analysis of 28S and 16SrDNA (Belshaw *et al.* 1999). The absence of fine submedial dorsal teeth on the larval mandible of *Microplitis* Foerster is most likely the result of its biology; the larvae emerge from an exposed host and consequently, the ectoparasitic phase (for which the toothed mandibles are used) is missing.
- 2) The second and more derived group has the hind coxae enlarged (Microgastrini; most basal group in Europe the genus *Cotesia* Cameron, which has vein r-m of fore wing lost).
- 3) The vein 1-SR of fore wing is pointing more apicad in the remainder of Microgastrini (i.e. excluding *Cotesia*).
- 4) The specialised shape and sculpture of first and second tergites, accompanied by the loss of vein r-m of fore wing characterise the next subgroup: *Protapanteles* Ashmead s.l.
- 5) The medial groove of the first metasomal tergite, with the grooves of second tergite parallel delimit the next subgroup: in the West Palaearctic region *Diolcogaster* Ashmead + *Deuterixys* Mason.
- 6) The specialisation on concealed living hosts (endoparasitoids of "Macrolepidoptera suite" of character-states) characterise the most derived subgroup. In the West Palaearctic region *Microgaster* Latreille and *Apanteles* Foerster; the latter has vein r-m of the fore wing lost.

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SYSTEMATICS STUDY AND BIOLOGICAL SURVEY OF MYMARIDAE FROM CHINA

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Abstract — The recent status of the systematic study and biological survey of Mymaridae from China is present in this paper. Based on an examination of the collected specimens, about 26 genera have been recognized from China. A key to genera of Chinese Mymaridae was illustrated and given in 2000. More than 40 species in 9 genera have been described. There are a large amount of specimens yet to be identified to species. In addition to the systematics, the surveys on biology and ecology of some common mymarids have been conducted. As the foundation of the study of Mymaridae in China is rather weak, much remains to be done. Any international cooperation and help will be much appreciated.

Key words: Mymaridae, systematics, biological survey, China

Introduction

Since Curtis first described the genus *Mymar* in 1832, about 130 genera and 1350 species of Mymaridae have been reported in the world. In this paper the author gives a brief account of the present status of the systematics study and biological survey of Mymaridae from China.

Although Profs. Chu Joo-tso and Liu Chong-le were the earlier pioneers who paid attention to the survey of natural enemies as well as the promotion of biological control. Studies on Chinese Mymaridae had started rather late in China. Profs. Chu Joo-tso and He Jun-hua, who were the first scientists, paid attention to some of the mymarids parasitizing in the eggs of rice leaf beetle (*Oulema oryzae*), rice leafhopper (*Nephotettix cincticeps*), brown rice plant-hopper (*Nilaparvata lugens*). A general survey of natural enemies and biological control had a fine stride of development under the direction of the Chinese Agricultural Ministry beginning from 1970's.

Systematics studies of Mymaridae in China, evolved in the follow way. Taguchi (1975–1978) described 5 genera, namely: *Chaetomymar* (1 sp.), *Mymar* (2 spp.), *Camptoptera* (2 spp.), *Himopolynema* (2 spp.), *Stephanodes* (1 sp.), and 8 species of Mymaridae from Taiwan province. Pang Xiong-fei and Wang Ye-an of South China Agriculture University reported 5 species of the genus *Anagrus* from south China in 1985. A collection of microhymenoptera collected from paddy fields and adjacent territories, citrus orchards, tea gardens and the Wuyishan Nature Reserve in Fujian Province has been established by us during 1979–1985 and about 15 000 specimens of Mymaridae have been obtained. Based on these specimens, a preliminary report on the classification of Mymaridae was given which included 14 genera of Mymaridae from south China (Lin 1986).

I had a good opportunity to visit Italy in 1994 and worked on the genera *Omyomymar* Schauff and *Anagrus* Haliday with Dr. Chiappini. Three new species of *Omyomymar* (Lin & Chiappini 1996) were described, 16 species of *Anagrus* were listed for China, which from 9 were new to

science (Chiappini & Lin 1998). Later, 2 new *Pseudanaphes* and *Camptopteroides* species were described (Lin 1997; Huber & Lin 1999).

After 1996, supported by the Natural Science Foundation of China, a large scaled collections from 23 provinces and regions of China has been made by us and about 80 000 specimens have been added.

Based on the examination of the collected specimens, about 26 genera have been recognized from China: *Acmopolynema* Ogloblin, *Alaptus* Westwood, *Anagroidae* Girault, *Anagrus* Haliday, *Anaphes* Haliday, *Arescon* Walker, *Camptoptera* Foerster, *Camptopteroides* Viggiani, *Chaetomymar* Ogloblin, *Cleruchus* Enock, *Dicopus* Enock, *Erythmelus* Enock, *Eustichus* Haliday, *Gonatocerus* Nees, *Himopolynema* Taguchi, *Litus* Haliday, *Mymar* Curtis, *Narayanella* Subba Rao, *Omyomymar* Schauff, *Ooctonus* Haliday, *Polynema* Haliday, *Pseudanaphes* Noyes & Valentine, *Ptilomymar* Annecke & Doutt, *Schizophagramma* Ogloblin, *Stephanodes* Enock, and *Stethynium* Enock. A key to genera of Chinese Mymaridae was illustrated and given in 2000 (Lin & Xu, 2000). More than 40 species in the genera *Acmopolynema*, *Anagrus*, *Camptopteroides*, *Chaetomymar*, *Himopolynema*, *Mymar*, *Narayanella*, *Omyomymar*, and *Pseudanaphes* have been recognized and described. There are a large amount of specimens yet to be identified to species, with possible description of new species.

In addition to the systematics, surveys on biology and ecology of some common mymarids in *Anagrus*, *Chaetomymar*, and *Gonatocerus* genera have been conducted also. Luo Xiao-nan & Zuo Wen-xi (1980) reported their research on the bionomics and utilization of mymarid egg parasitoids of rice plant-hoppers. In Shaxian of Fujian, 9 species of egg parasitoids of rice plant-hoppers have been found, including *Anagrus flaveolus* and 4 *Anagrus* spp., *Gonatocerus longicrus*, *Paracentrobia andoi*, *Oligosita nephotettica*, and *Panstenon* sp. (Pteromalidae). From the observation, it has been found that the eggs of plant-hoppers in graminaceous weeds are important alternative hosts of these parasitoids during the winter. It suggested that protection of parasitoid resources in field graminaceous weeds must be made.

Zhao Shi-xi, Zuo Wen-xi & Luo Xiao-nan (1993) studied the resource niche of mymarid egg-parasitoid of rice plant-hoppers. The niche breadth, overlap and similarity percentage of 3 *Anagrus* species: *A. nilaparvatae*, *A. longitubulosus*, and *A. paranilaparvatae*, of rice plant hoppers were estimated by means of investigating their resource niche in paddy fields. After that, the conservation of *Anagrus* spp. in the natural control of rice plant-hoppers were discussed according to the niche theory.

Lou Yong-gen *et al.* (1996) observed the antennal sense organs of *Anagrus nilaparvatae* by using scanning electron microscope. Five types of sensilla were found, namely trichoid sensilla (I, II), placoid sensilla, clubbed sensilla, swordlike sensilla, and Bohm's bristles on the female antennae of *Anagrus nilaparvatae*. However, trichoid sensilla II and clubbed sensilla were not found on the male antennae. Also, the number and distribution of the sensilla were obviously different between two sexes.

Lou Yong-gen *et al.* (1996) reported the behavioral response of *Anagrus nilaparvatae* to the volatile of rice varieties. The study was carried out using 4-arm olfactometer and the results showed that the behavioral response of the parasitoid, *Anagrus nilaparvatae*, to the volatile of various rice varieties was obviously different. Attractiveness of the volatile from undamaged rice plant of Z852 and TN1 to the parasitoid was significantly stronger than that of Nabeshi. After rice plants were damaged by brown plant-hopper (BPH), *Nilaparvata lugens* (Stal), the difference of attractiveness to the parasitoid among rice varieties increased significantly. Within the same variety, the

behavioral response of the parasitoid to rice plant damaged by BPH was highly greater than that of undamaged rice plant. However, no difference was found between the volatile of rice plant-BPH nymph complex and that of rice-BPH egg and female complex.

Lin Shi-chi & Luo Xiao-nan(1996) gave their preliminary survey on the parasitoids of *Nephotettix cincticeps* in Fujian. Among the 3 egg parasitoids found, 55.7% were represented by 2 *Gonatocerus* species and 40.7% – by *Paracentrobia andoi*.

In order to find the egg parasitoids of *Sophonia* spp. from their native habitat for the classical biological control in Hawaii, exploratory study on the natural enemies, especially on egg parasitoids, of *Sophonia* spp. in Fujian were conducted by me and my students in recent years. Three predators and 12 parasitoids had been found in Fuzhou. Besides 1 Dryinidae species parasitizing the nymphs, other 11 species are egg parasitoids. Among them, 6 species are Mymaridae (2 species of *Chaetomymar*, 2 species of *Gonatocerus*, 2 species of *Polynema*), 4 of them are *Hispidophila* spp., *Ufens rimatus* and *Oligosita* sp. in Trichogrammatidae and 1 species is *Centrodora* sp. of Aphelinidae. *Chaetomymar bagicha* and *Ch. hishimoni* are the most dominant egg-parasitoids, which account for 65.8 % in the 11 egg parasitoids discovered. They are followed by *Gonatocerus* and *Polynema* species. Other parasitoids are very rare.

The seasonal abundance of parasitoid population differed significantly. Parasitoid population was greater from September till November. The egg parasitism increased progressively from spring to fall. Parasitism in September could reach 91.4%, which is the largest peak throughout the year. The mean parasitism from April to November is 61.9%, with a lowest parasitism 31.0%. The parasitoids are fond of laying their eggs into the early and mid embryonic stage (less than 10 days) *Sophonia* eggs. Within 5 to 10 days host eggs lure time, the parasitism increased obviously with the lure time prolonged. But the parasitism cannot be increased after the host eggs exposed for more than 10 days (Chen & Lin 2000).

Different ecological environment of orchard causes the different species of egg parasitoids and parasitism. The abundance of vegetation leads to the abundance of *Sophonia* leafhoppers and also promotes the development of natural enemies at same time and thus improves the control efficiency for pests.

As is evident from the above, the foundation of the study of Mymaridae in China is rather weak. Much remains to be done. We are willing to cooperate and invite entomologists to our institutions to study Mymaridae, Trichogrammatidae and other parasitic Hymenoptera. Any international cooperation and help will be much appreciated.

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SYSTEMATICS STUDIES OF PARASITIC HYMENOPTERA IN INDIA

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Abstract – Though India contains many interesting endemic fauna of parasitic hymenoptera very little has been done on the taxonomy of several groups. There are two very important biodiversity hot spots in India viz. Western Ghats and North East areas. Only very few centres in India are engaged in taxonomic studies of parasitic hymenoptera. They are Systematic Entomology Laboratory of Department of Zoology, University of Calicut, Kerala state, Zoological Survey of India, Calcutta, Indian Agricultural Research Institute, New Delhi and Department of Zoology Aligarh Muslim University etc. Unfortunately the conservation strategies in India often give impediments in collecting insects here. Chalcidoidea and Ichneumonoidea are the two better worked out superfamilies in India.

Key words: Hymenoptera, Parasitica, India, taxonomy

Introduction

Parasitic Hymenoptera constitute one of the most important and species-rich groups of Hymenoptera (LaSalle 1993). It includes many species that prevent the excessive increase of many other species of insects and arachnids. A few parasitic hymenopterans are harmful being phytophagous pests of agricultural crops or other useful plants and as hyperparasitoids attacking beneficial parasitoids. Many parasitic Hymenoptera are used as efficient biological control agents against insect pests. Several species of parasitic hymenopterans in India are key stone species and removal of such keystone species is causing cascade effect in India. India is a paradise of parasitic Hymenoptera diversity.

This interesting and rich fauna should be explored and studied before attempting to take steps to conserve them. In this paper I have tried to give a picture of the present status of taxonomy of Indian parasitic Hymenoptera and about the future scope of taxonomic studies.

Classification and biological diversity

The Order Hymenoptera is divided into two suborders viz. Symphyta and Apocrita. The latter is divided into two divisions viz. Aculeata and Parasitica the members of 'Parasitica' are known as Parasitic Hymenoptera (*sensu stricto*) and includes 11 Superfamilies showed in the Table 1.

Distribution

Parsitic Hymenoptera are widely distributed all over India. The fauna of northern end especially of Kashmir and Himachal Pradesh are very much related to Palaearctic fauna. The fauna of

Table 1 The approximate number of known species and genera in India

Superfamily	Genera number	Species number
Ichneumonoidea	550	2000
Chalcidoidea	550	1800
Platygastroidea	50	200
Proctotrupeoidea	24	55
Ceraphronoidea	2	4
Evanioidea	10	62
Cynipoidea	?	51
Trigonalyoidea	?	6?
Stephanoidea	5	13
Mymarommatoidea	0	0
Megalyroidea	0	0

Peninsular India shows affinities to Srilankan and nearby islands like Seychelles, partly to eastern Africa. The parasitic Hymenoptera of the Andaman and Nicobar Islands are very much related to South Est Asian fauna. As such the Indian parasitic Hymenoptera have close affinity to the fauna of the rest of the Oriental region. Several genera of Australian region are met with in India.

India has two important hot spot areas of biodiversity viz. the Western Ghat region and the Valleys of North East Himalayan region. There are 10 % threat to the fauna by way of habitat destruction and fragmentation. It is estimated that about 30-40 % of parasitic Hymenoptera species await discovery in the Indian subcontinent and if strong measures to prevent these destruction and fragmentation of habitats are not taken urgently, the majority of these 30-40% undiscovered fauna will be extinct before they are discovered and described.

Endemic and introduced species

The Indian fauna of parasitic Hymenoptera contains more than 50 % endemic species. It is roughly estimated that about a dozen of species of parasitic Hymenoptera found in India are emigrant species, which came from nearby zoogeographical regions. The number of threatened and endangered species is not known.

Conservation of Parasitic Hymenoptera

Preventing taxonomists to collect insects is not a method for conserving parasitic Hymenoptera or any other fauna or flora. Before taking steps to conserve the fauna and flora one has to know what is to be protected and what is not to be protected (Narendran 2001). For this taxonomic studies are absolutely essential. It is absolutely foolish to compare the methods of conservation of vertebrates and invertebrates like insects. For insects preservation of the natural habitat is the first

and foremost important step for conservation. The second important step is to stop the indiscriminate use of pesticides for controlling pests. Dusts have long been known to have an adverse effect on parasitic Hymenoptera (Bartlett 1951; LaSalle 1993). Hence methods for saving parasitic Hymenoptera from the dust should be developed specially in India where several agricultural fields are situated near the roadside. If the above stated measures are properly carried out much of our insect fauna will be saved provided taxonomists collect and identify the various species existing in their countries. Without collecting insects, taxonomists cannot identify from field observation (as in the case of vertebrates) alone of many minute insects which are often less than 1 mm in length. The forest officials as well as other authorities should remember this fact before formulating rules, which will prevent taxonomists from collecting insects. When the taxonomists identify any threatened species or endangered species of insect, germplasm of such species can be preserved if necessary. Systematics is important for understanding factors determining the abundance and diversity of different species making up the living world (Narendran 2000).

Future prospects

Taxonomic research is being carried out only on 4 or 5 superfamilies in India and the other superfamilies need attention of Indian taxonomists (Table 2). Among the various institutions in

Table 2 The following table mentions the major research centres engaged in taxonomy of parasitic Hymenoptera in India

Superfamily	Centres of Taxonomic Research
Ichneumonoidea	Zoological Survey of India, Calcutta, W.B. Dept. of Zoology, Marathwada University, Aurangabad, MH Dept of Zoology, University of Calicut, Kerala Dept. of Zoology, Aligarh Muslim University
Chalcidoidea	Dept of Zoology, University of Calicut, Kerala Zoological Survey of India, Calcutta, Kerala Dept. of Zoology, G.B. Pant University of Agriculture, U.P. Dept. of Zoology, Aligarh Muslim University Institute of Rain and Moist Forest Research, Jorhat, Assam
Proctotrupoidea	Dept of Zoology, University of Calicut, Kerala
Platygasteroidea	Dept of Zoology, University of Calicut, Kerala Dept of Zoology, Division of Entomology, College of Horticulture, Vellanikara, Kerala Dept. of Zoology, Government Post-graduate College Rishikesh
Stephanoidea	Dept of Zoology, University of Calicut, Kerala
Trigonalynoidea	—
Evanoidea	—
Cynipoidea	—
Megalyroidea	—
Mymarommatoidea	—
Ceraphronoidea	—

India, the Systematic Entomology Laboratory of the Department of Zoology, University of Calicut is the first in the rank for concentrating the taxonomic research in various families. It is followed by the Department of Zoology, Aligarh Muslim University. This also reveals that very few scientists and very few institutions are at present engaged in the taxonomic work on parasitic Hymenoptera.

On the whole we have to go a long way to complete revisions of all families of parasitic Hymenoptera of Indian subcontinent. The number of Indian workers of parasitic Hymenoptera need to be multiplied at least ten times or more if the fauna is to be explored, systematic research conducted and research monographs published. Our hindrances are enormous and the task is tremendous. The immediate need is to develop taxonomic centres staffed with well-trained taxonomists in different parts of India with sufficient support to build up a good collection of specimens and literature. Since parasitic Hymenoptera is a high priority group (LaSalle & Gauld 1993) for studying the taxonomy and biodiversity we must take every effort to encourage such research by giving all facilities and funding.

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THE BASAL LINEAGES OF MYMARIDAE (HYMENOPTERA) AND DESCRIPTION OF A NEW GENUS, *BORNEOMYMAR*

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Abstract – Mymaridae with 5-segmented tarsi and an 8-segmented antennal funicle in females are putatively primitive. They include the extant genera *Boudiennia*, *Eustochomorpha*, *Gonatocerus*, *Ooctonus*, and one new genus, *Borneomymar*, **gen. nov.**, with three new species *B. discus* **sp. nov.**, from Borneo, *B. madagascar* **sp. nov.**, from Madagascar, and *B. primitivum* **sp. nov.**, from Sulawesi. Relationships of these genera are discussed and summarized in an intuitive cladogram.

Key words: *Borneomymar*, new genus, primitive Mymaridae, relationships

Introduction

About 15 of the approximately 100 extant genera of Mymaridae have 5-segmented tarsi. They have often been grouped together because they share this feature (e.g. Förster 1847; Debauche 1948; Schauff 1984; Yoshimoto 1990). Annecke & Doutt (1961), and Subba Rao & Hayat (1983), however, placed them in two subfamilies and Viggiani (1989) placed them in three subfamilies. Four of the genera, *Boudiennia*, *Eustochomorpha*, *Gonatocerus*, and *Ooctonus* have females with an 8-segmented antennal funicle. The former two genera were so poorly known that they have been mentioned only once each since their description (Annecke & Doutt 1961; Yoshimoto 1975). The latter two genera, both widespread, were generally treated as the most primitive in the family and were grouped or keyed together, though Schauff (1984) correctly recognized that such a grouping is based on symplesiomorphies. I recently examined the types and a few additional specimens of *Boudiennia* and *Eustochomorpha* as well as specimens representing one new genus, described below, that also has an 8-segmented funicle and 5-segmented tarsi. Studying this material has helped resolve relationships among the primitive genera. Their putative relationships are discussed and summarized in a cladogram.

Methods

Specimens received in ethanol were critical point dried and card mounted. Three males and one female of one of the new species and a female of another were dissected and slide mounted in Canada balsam for description. Terminology follows Gibson (1997): fu_n refers to funicle segment and Gt_n , St_n refer to gastral terga and sterna, respectively. Measurements are in micrometers.

Type specimens are deposited in the following institutions: BMNH, The Natural History Museum, London; CNCI, Canadian National Collection of Insects, Ottawa; MZLU, Museum of Zoology, Lund University, Lund; and UCDC, Bohart Museum of Entomology, University of California, Davis.

Borneomymar Huber, gen. nov.

Diagnosis. Female antenna with 8 funicle segments and 1-segmented clava. Forewing venation at least 0.6 X wing length. Marginal vein 2.0 X as long as submarginal vein, with hypochaeta much closer to proximal than to distal macrochaeta. Stigmal vein short, ending in triangular stigma at least half as wide as long. Postmarginal vein as thick as marginal vein, at least 5 X as long as stigmal vein. Tarsi 5-segmented. Gastral petiole of female shorter than wide.

Description. Female. Head length 0.6-0.8 X width. Face without subantennal grooves. Toruli at least half their length from transverse trabecula. Pronotum entire. Propleura abutting anteriorly. Prosternum divided longitudinally. Prepectus a uniformly broad band reaching midline ventrally. Mesoscutum 1.3-1.7 X as wide as long, with straight or slightly curved notauli. Scutellum about 0.66-0.89x mesoscutal length, with posterior scutellum slightly shorter to slightly longer than anterior scutellum. Axillae in line with anterior margin of scutellum or, in *B. primitivum*, advanced. Dorsellum distinct, diamond-shaped. Forewing 3.8-4.4 X as long as broad, with venation extending at least 0.6 X wing length. Stigma distinct, triangular. Marginal vein much longer than submarginal vein. Postmarginal vein over 5 X stigmal vein length. Propodeum about half length of mesoscutum. Gt_1 length at most 1.3 X Gt_2 . Gaster with spiracle on Gt_6 . Cerci exerted, on digit-like protruberance.

Male. Known only for *B. discus*. Antenna with 11 flagellar segments, the basal segment without longitudinal sensilla, the others with about 4 unevenly arranged, short longitudinal sensilla (6 on last segment). Head length about 0.8 X width. Gena in lateral view twice as wide as small eye. Pronotum visible in dorsal view, about 0.4 as long as mesoscutum. Metasoma 1.6 X length of mesosoma. Petiole at most 1.7 X as long as wide. Gt_1 shorter than Gt_2 . Spiracle absent. Genitalia encapsulated.

Type species: *Borneomymar discus* Huber.

Etymology. The genus is named from Borneo, the island of origin of the type species plus *Mymar*. Gender: neuter.

Discussion. *Borneomymar* contains two similar species and a third, morphologically quite different one. *Borneomymar discus* and *B. madagascar* look like many *Australomymar* species, particularly because of ovipositor length. In contrast, *B. primitivum* looks more like a species of *Arescon*, based on wing structure, number of mandibular teeth, and the advanced axillae. Initially, I considered placing *B. primitivum* in a separate new genus because it seemed to be more closely related to *Arescon* than to *Australomymar*. However, variation in size and body shape in *Australomymar* and perhaps also among *Arescon* can be as great as among the three *Borneomymar* species. I therefore conclude that it is best at present to place all three new species in *Borneomymar*. *Australomymar* spp. differ from *Borneomymar* by having 4-segmented tarsi and, in females, 6-segmented funicle. *Borneomymar discus* and *B. madagascar* appear to form a link between *Eustochomorpha*, the most primitive genus of Mymaridae, and *Australomymar*, probably the most primitive genus with 4-segmented tarsi. *Arescon* spp. differ from *Borneomymar* by having a 5-segmented funicle in females and by lacking a postmarginal vein. Males of *B. primitivum* are needed to compared their genitalia with the distinctive male genitalia of *Arescon* (Viggiani 1988) to better determine whether *B. primitivum* forms a link with *Arescon* and might better be classified as its sister genus. The biology of *Borneomymar* spp. is unknown. The large body size, extremely long ovipositor, and the fact that one species of the related genus *Australomymar* is known to

parasitize Tettigoniidae suggests that *B. discus* and *B. madagascar*, at least, might parasitize Orthoptera eggs deeply imbedded in plant tissue.

***Borneomymar discus* Huber, sp. nov.**

(Figs 1, 3, 4)

Type material. Holotype (BMNH) on card labelled: 1."Sarawak: Gunong Mulu Nat. Park R.G.S. Exped. 1979". 2. "Holotype *Borneomymar magnificum* Huber 2001". **Paratypes.** Malaysia: Sabah, Sipitang Mendolong. T1B/W4 31.III.1989 leg. S. Adebratt (1? on card, MZLU); Sarawak, sw. Gunung Buda, 64 km S. Limbang, 4°13'N 114°56'E, 8-15, 16-21, and 22-28.xi.1996, S.L. Heydon & S. Fung, MT (1 & 2 on points, 1 & 2 on slides, CNCI, UCDC).

Description. Female. Body length 1562-2200 (n=4). Head, mesosoma, except brown lateral panel of mesoscutum, and legs, except sometimes hind tibia, honey yellow; antenna, except yellowish pedicel and fu₁, hind tibia and metasoma brown. Forewing (Fig. 3) mainly brown except base behind submarginal vein, and anterior and posterior margins beyond stigma hyaline. Hind wing brown.

Antenna (Fig. 4) with radicle about 0.33 X as long as scape. Scape enlarged in basal half. Length measurements (n=1): scape 402, pedicel 86, fu₁-fug 139, 187, 135, 114, 103, 96, 94, 88, clava 248. Fu₄-fug each with 2 longitudinal sensilla. Clava with 7 longitudinal sensilla in apical



Figure 1 *Borneomymar discus*, paratype female, lateral, habitus digital image

half. Gena about 0.13 X eye width (28: 217). POL 1.1 X OOL and 1.6 X LOL. Mandibles with 3 teeth. Pronotum mostly hidden in dorsal view. Setae of thorax short, with 2 or 3 pairs on pronotum and 1 pair on each of mid- and lateral lobes of mesoscutum, axilla, anterior scutellum and metanotum. Propodeum with 1 pair of setae. Forewing (Fig. 3) length (n=1) 2134, width 493, with venation 0.61 X wing length. Submarginal vein 455, marginal vein 814 and with 1 distal macrochaeta, stigmal vein 52, postmarginal vein 333 (from pinned paratype, UCDC). Hypochaeta next to proximal macrochaeta. Petiole length 20, width 80. Gaster about 1.8 times mesosomal length, in dorsal view strongly compressed, in lateral view circular (Fig. 1), its length 1152, width 168, height 960. Lengths of Gt₁ - Gt₆ (measured along lateral midline): 363, 275, 216, 242, 130, 47. Cercus with two of the setae over 2.5 X as long as the remainder. Ovipositor forming a large loop inside gaster, then extending about 4500–5000 beyond hypopygial apex.

Male. Body length 1675-2760 (n=4). Colour as for female but top of head brown. Lengths of petiole and Gt₁ - Gt₆: 104, 187, 229, 256, 238, 220, 232, 148, 38. Anterior and posterior margins of terga strongly sinuate.

Specific epithet. Latinized from the Greek noun *diskos*, a flat, circular plate, referring to the shape of the gaster.



Figure 2 *Borneomymar madagascar*, holotype, dorsal, habitus digital image

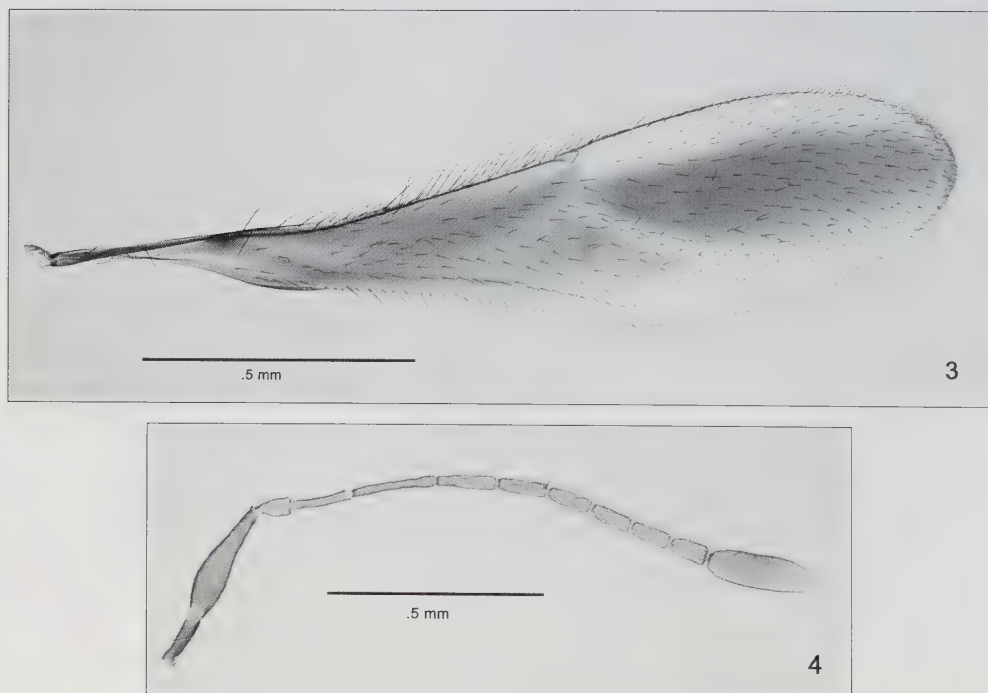
Borneomymar madagascar Huber, sp. nov.

(Fig. 2)

Type material. **Holotype** ?(UCDC) glued to a card point and labelled: 1."Madagascar, Antsiranana, 11 km WSW. Befingotra Res. Anjanaharibe-Sud 14°45'S 49°27'E, 16-22.XI.1994 B.L. Fisher #1231". 2."Holotype *Borneomymar madagascar* Huber 2001". The holotype has the right antenna beyond the pedicel missing.

Description. Female. Body length 1211 (n=1). Body brown (Fig. 2) with following yellowish: scape, pedicel, fu_1 , legs except hind tibia, apex and base of gaster. Wings hyaline. Antenna with radicle about 0.12 X as long as scape. Scape symmetrical, widest at midpoint. Length measurements: scape 84, pedicel 59, fu_1 – fug 89, 99, 109, 99, 89, 89, 89, 84, clava 188. Longitudinal sensilla not visible under stereoscope at 160X. Gena about 0.4 X eye width (59: 138). POL 1.2 X OOL and 2.0 X LOL. Mandibles with 3 teeth. Pronotum visible in dorsal view, about 0.4 X mesoscutal length (69: 168). Setae of mesosoma very short (not clearly visible at 160 X). Propodeum with 1 pair of setae. Forewing length 1280, width 282, with venation 0.68 X wing length. Submarginal vein 277, marginal vein 386 and with 1 distal macrochaeta, stigmal vein 27, postmarginal vein 217. Hypochaeta about one fifth distance from proximal macrochaeta towards distal macrochaeta. Petiole length 20, width 45. Gaster about 1.1 X mesosomal length, its length 538, width 205, height 256. Cercus with setae subequal in length. Ovipositor exerted 2660 beyond hypopygial apex.

Specific epithet. The species is named from Madagascar, the island of origin.



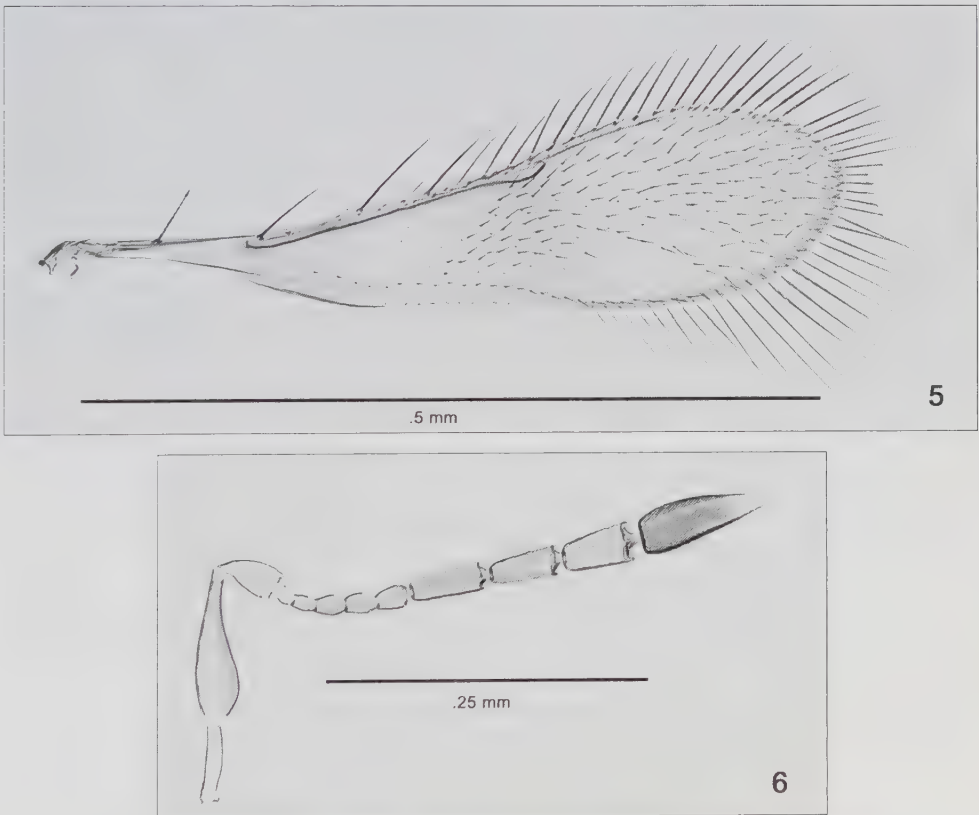
Figures 3–4 *Borneomymar discus*, paratype female: 3, forewing; 4, antenna

Borneomymar primitivum Huber, sp. nov.

(Figs 5, 6)

Type material. Holotype (BMNH) dissected under 4 coverslips on slide in Canada balsam and labelled: 1."Indonesia: Sulawesi, Utara, Dumoga-Bone NP, Toraut, v.1985, 210 m, J.S. Noyes, swept". 2."*Borneomymar primitivum* Huber 2001". **Paratype.** Same data as holotype but vii.1985, N.E. Stork, canopy fog #13" (1? on point, BMNH).

Description. Female. Body length 717. Body pale yellow and creamy-white; dark brown are clava except apex, mouth rim, pro-, meso- and metapleura, and apical tarsomere of each leg; creamy white are fu_6 and fu_7 , pronotum, scutellum, coxae, and gaster except brown Gt_5 and ovipositor. Forewing hyaline except for pale brown setose area behind apex of venation and along posterior margin at base. Hind wing hyaline. Antenna (Fig 6) with radicle 62, about 0.34 X as long as scape. Scape enlarged in basal half. Length measurements ($n=1$): scape 184, pedicel 50, fu_1 – fug 16, 16, 23, 26, 29, 62, 59, 63, clava 120. Fu_6 – fug each with 2 longitudinal sensilla. Clava with 5 longitudinal sensilla. Gena about 0.1 X eye width. $POL \approx 0.5$ X OOL and ≈ 2.0 X LOL (under stereoscope at 160X). Mandibles with 4 teeth. Mesosoma length 98. Pronotum clearly visible in



Figures 5–6 *Borneomymar primitivum*, holotype: 5, forewing; 6, antenna

dorsal view. Setae of thorax short, with 3 pairs on pronotum and 1 pair on each of mid- and lateral lobes of mesoscutum and on metanotum. Propodeum with 1 pair of setae. Forewing (Fig 5) length 583, width 154, without microtrichia along hind margin beyond venation and in triangular area behind marginal vein, except for cubital setal line. Venation ~445. Submarginal vein 105, marginal vein 212 and with two distal macrochaeta, stigmal vein 30, postmarginal vein ≈ 128 . Hypochaeta about one quarter distance from proximal macrochaeta towards first distal macrochaeta. Petiole length 14, width 37. Gaster length 356, width 198, height 180, about 1.2 X length of mesosoma. Lengths of Gt₁–Gt₆: 45, 40, 49, 66, 59, 80. Anterior and posterior margins of terga straight. Cercus with one of the setae crooked and over 2.5 X as long as the next longest seta. Ovipositor straight, extending slightly (about 80) beyond gastral apex.

Specific epithet. Latin adjective, primitivus -a, -um, meaning first.

Discussion

Finding apomorphies to demonstrate that the various supraspecific taxa of Mymaridae are monophyletic is difficult. Many of the character states observed result from reductions, fusions, or loss, so they are prone to homoplasy. Schauff (1984) recognized this when he presented the first and only cladogram of relationships within Mymaridae. Because he treated only the 26 genera known at that time from the Holarctic region only two of the putatively primitive genera, (those with 8 funicle segments and 5 tarsomeres) were included: *Gonatocerus* and *Ooctonus*. Only one intuitive cladogram is proposed here (Fig. 7). It includes the five described, extant genera with the above combination of symplesiomorphies, and *Triadomerus*, represented by cretaceous fossils from Canada, and extant (but undescribed) Australian species. The non-terminal stems are labelled from 1-13 and discussed. Other relationships among the primitive genera could be hypothesized and supported by apomorphies (mostly as homoplasies), but a detailed analysis cannot be done until all useful characters are discussed and their states coded for all mymarid genera.

Stem 1 is based on a unique, apomorphic state that defines the family Mymaridae. The vertex is separated as a distinct sclerite from the face by sutures and associated cuticular thickenings, the trabecula, above the toruli and next to the dorsal orbit of each eye.

Stem 2 leads to two genera. I have found no apomorphies to define the lineage, hence the trifurcation. The genus *Triadomerus*, the most primitive genus of the family, retains the putative ground plan flagellar formula of 11 segments in both males and females (8 funicular and 3 claval segments in females). *Eustochomorpha* is separated from *Triadomerus* by one homoplasy: reduction in number of claval segments from 3 to 2. This Australian genus, with one species, is known only from females. *Triadomerus* may be a synonym of *Eustochomorpha*.

Stem 3 has one apomorphic state change: reduction in number of flagellar segments in females to at most 9. The flagellum may consist of 4 to 8 funicular segments and 1-3 claval segments. Genera with 8 funicle segments, however, only have a single claval segment. Females of all mymarids except *Triadomerus* thus have fewer flagellar segments than males. Males of a few genera may also have a reduced number of flagellar segments (as few as 7 in some *Camptoptera*).

Stem 4 leads to two genera: *Borneomymar* and *Australomymar*. I have found no apomorphies to define the lineage. *Australomymar* is separated from *Borneomymar* by two homoplasies: reduction in number of tarsomeres from 5 to 4 and funicle segments from 8 to 6.

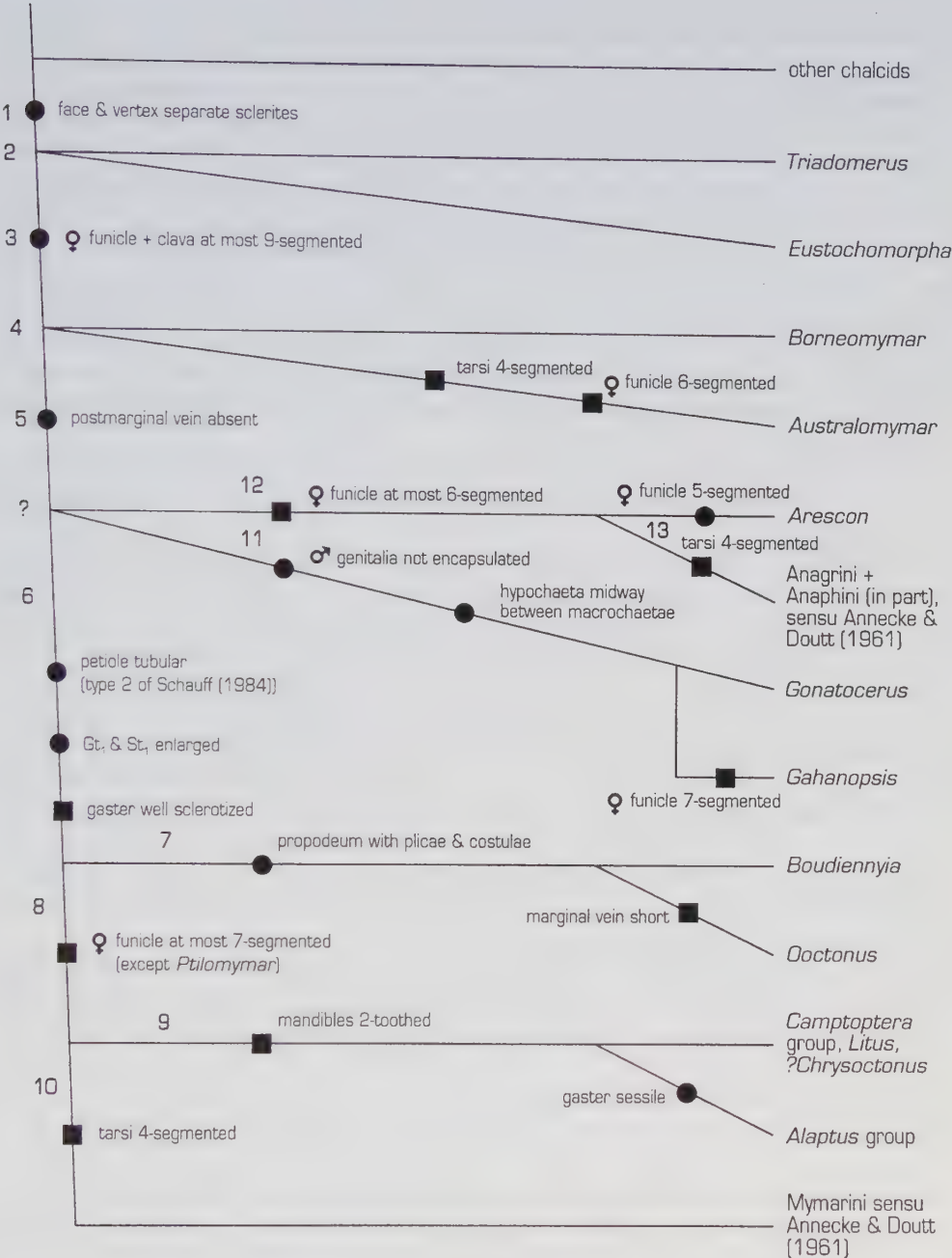


Figure 7 Cladogram of putative relationships among genera of Mymaridae with 5-segmented tarsi

Stem 5 has one apomorphic state change: loss of the postmarginal vein. It leads to an unresolved trifurcation.

Stem 6 is defined by three apomorphies: elongate, tubular petiole into which the base of Gt_1 projects (petiole type 2 of Schauff 1984), Gt_1 and St_1 enlarged, and a well sclerotized gaster. These apomorphies may be homoplasious, occurring also in some species of *Gonatocerus* (stem 11). There is a reversal in one of them (size of Gt_1 and St_1) in the *Alaptus* group (stem 9).

Stem 7 is defined by one apomorphy: propodeum with plicae and costulae. The widespread genus *Ooctonus* is separated from *Boudiennya*, found so far only in Australia and New Caledonia, by one homoplasy: a short marginal vein, with the venation much less than half the wing length.

Stem 8 is defined by one homoplasy: reduction in number of funicle segments from 8 to 7 or fewer, except in *Ptilomymar*, which retains an 8-segmented funicle but has 4-segmented tarsi.

Stem 9 is defined by one homoplasy: mandibles with at most 2 teeth. The *Alaptus* group of genera is separated by from the others by at least one apomorphy: a short and wide, ring-like petiole that makes the gaster appear sessile. Within the *Camptoptera* group, *Eofoersteria* is distinguished by one homoplasy: reduction (by fusion) in tarsomere number from 5 to 4. *Litus* also belongs here, and possibly other genera such as *Chrysoctonus*.

Stem 10 is defined by one homoplasy: reduction in number of tarsomere from 5 to 4. This lineage contains the putative genera placed by Annecke & Doutt (1961) in their Mymarini and others described since.

Stem 11 is a monophyletic lineage defined by two synapomorphies: male genitalia unencapsulated (Viggiani 1988) and hypochaeta midway between proximal and distal macrochaeta. *Gahanopsis*, from the Neotropical region, is separated by one homoplasy (a 7-segmented funicle) from *Gonatocerus*, which contains well over 250 nominal species in several distinct species groups.

Stem 12 is defined by one symplesiomorphy and is likely paraphyletic. No apomorphies have been found to define it. How this lineage relates to lineages 6 and 11 is uncertain. Symplesiomorphies shared with *Eustochomorpha*, *Borneomymar* and *Australomymar* include an encapsulated male genitalia, hypochaeta next to basal macrochaeta, and pronotum entire. Symplesiomorphies shared with stem 11 are the unmodified petiole, the relatively poorly sclerotized gaster, and Gt_1 and St_1 similar in size to the remaining terga and sterna. *Arescon* is the sister group to the remaining genera and is defined by one apomorphy, its 5-segmented funicle and perhaps also by structure of the male genitalia.

Stem 13 is defined by a reduction in number of tarsomeres from 5 to 4. This lineage contains all of the putative genera placed by Annecke & Doutt (1961) in their Anagrini and Anaphini (in part - *Anagroidea* belongs in lineage 6), as well as others described since.

Conclusions

Eustochomorpha is the most primitive, extant mymarid genus. Other genera with 5 tarsal segments, 8 funicle segments in females, and 11 flagellar segments in males form the bases of three separate lineages, two of which appear to be monophyletic. All extant, primitive mymarid genera are represented in the southern hemisphere, particularly in the Australian region, which contains all the genera except *Borneomymar*. This region is unlikely to be the centre of origin of Mymaridae

because Cretaceous fossils of the primitive genus *Triadomerus* (Yoshimoto 1975) have been found in Canadian amber. Instead, the Australian region, and also southern South America contains a relict fauna that survived since the Cretaceous but largely died out elsewhere. A good understanding of this Gondwanan fauna is therefore required to develop a sound higher classification within the family to update and, if necessary, replace that proposed by previous authors.

Acknowledgements

I thank J. Noyes (BMNH), R. Danielsson (MZLU), S. Heydon (UCDC) for lending me material of the new species. Particular thanks are offered to J. Noyes for recognizing two of the new taxa and drawing my attention to them. J. Cardale, Australian National Insect Collection, Canberra, gave me access to the extensive mymarid holdings there and loaned me specimens of *Boudiennyia*. C. Burwell, Queensland Museum, Brisbane, let me examine the types of *Eustochomorpha* and *Boudiennyia* from the Girault collection. Klaus Bolte prepared the digital images and plates.

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SAMPLING GROUND OR TRULY MONOPHYLETIC? CLADISTIC ANALYSES APPLIED TO THE PHYLOGENY OF PTEROMALIDAE (HYMENOPTERA: CHALCIDOIDEA)

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Abstract — The phylogeny of the Chalcidoidea is still poorly understood and therefore still regarded as highly unstable. For a revised classification of the superfamily, the status of the Pteromalidae is considered to be of high priority. Membership in the Pteromalidae is largely based on exclusion, and therefore it is still unclear whether the Pteromalidae are truly monophyletic or not. Cladistic analyses were applied to resolve this question and to find possible monophyletic taxa and sister group relationships within the Chalcidoidea. The analyses were based on 90 merely morphological characters including 38 taxa from various pretended basal chalcidoid families. Due to taxonomical problems, the genus level was chosen for the analyses. The results strongly indicate that the pteromalids do not represent a natural taxon. The major subfamilies, Pteromalinae and Miscogasterinae, appear to be polyphyletic, with the tribe Pteromalini being monophyletic. The analyses indicate that the Spalanginae and Asaphinae are of the most ancient taxa among the Pteromalidae. The systematic placement of further pteromalid taxa remains unsolved at this time.

Key words: cladistics, phylogeny, Chalcidoidea, Pteromalidae

Introduction

The Chalcidoidea are still causing many taxonomical problems. The species richness, Noyes (1998) listed 21,248 valid species in 2040 genera, as well as the enormous morphological diversity and high plasticity of its members makes it difficult to deal with this superfamily. The biological diversity of this group is unrivaled. Chalcid wasps, for example, parasitize about the same number of orders than the rest of parasitic Hymenoptera taken together (Gibson 1993). All these findings have resulted in many different classifications which have been reviewed extensively by Bouček (1988b) who also describes the history about the Chalcidoidea taxonomy. Gibson (1993) remarked that there is still no consensus for a family classification of the Chalcidoidea. All existing classifications are mainly based on phenetical similarity, they are only rarely based on synapomorphies (Gibson 1993). Attempts to investigate the phylogeny of the Chalcidoidea applying rigorous methods of phylogenetic analyses are lacking (Bouček 1988a). If the superfamily was investigated, it was usually studied at the level of smaller taxa, like genera or subfamilies (e.g. Heraty & Darling 1984; Delvare 1988; Heydon 1988, 1989, 1997; Gibson 1989; Huang 1993; Grissell 1995). In order to solve the taxonomical problems to establish a stable higher classification, however, it is absolutely necessary to study the evolution of higher categories (Ronquist 1999). In this context, the Pteromalidae are thought to play a key role in the history of the Chalcidoidea. It is the third largest family in the Chalcidoidea with 3364 species in 588 genera.



There are 31 subfamilies, of which 16 are represented by just one or two genera (Noyes 1998). This classification indicates that one may find the highest morphological diversity in the Pteromalidae along with a manifold biology. The Pteromalidae are not defined by any unique character or combination of characters. The membership of this taxon is largely based on exclusion (Gibson 1993). For this reason the pteromalids are sometimes called “sampling ground”, “dumping ground” or something along this line.

Another aspect highlighting the unsolved taxonomical problems is the fact that the evolution of character states is unclear in most cases. We do not know which features are plesiomorphic and which are apomorphic (Gibson *et al.* 1999). In order to understand the evolution of the whole superfamily and to establish a stable classification for the Chalcidoidea, it is necessary to find synapomorphies that can help to define monophyletic groups. It was our aim to solve these questions and to arrive at a conclusion whether the Pteromalidae are truly monophyletic or whether they are the “sampling ground” within the Chalcidoidea. Furthermore, we tried to find possible relationships and sister taxa in the studied groups.

Materials and Methods

The investigated chalcid wasps were taken from the author's own collection or, mainly as dried and mounted specimens, from the entomological collection of the Zoological Museum of the University of Hamburg, Germany. 90 merely morphological characters were examined, of which 35 have been “two-state” and 55 “multi-state” characters (see appendix 1). Many character states of some taxa were examined using Scanning Electron Microscopy (CamScan DV4). To avoid *a priori* hypotheses in the evolution of character states, all “multi-state” characters were run as unordered characters. Questionable or invisible character states due to broken or badly mounted specimens were given a question mark. The resulting coding can be found in the Table 1, appendix 2.

Due to the species' richness found in chalcid wasps on one hand and the unstable classification on the other hand, the genus level was chosen as the operational taxonomic unit. *Eurytoma* Illiger (Eurytomidae) and *Brachymeria* Westwood (Chalcididae) were chosen as outgroup taxa because of their membership in two of the most ancestral regarded families (Bouček 1988a). The 36 ingroup taxa belong to the families Torymidae, Ormyridae, Eucharitidae, Perilampidae, and Pteromalidae. These non-pteromalids were included, because the idea that they are closely related to the Pteromalidae is widely discussed (Heraty & Darling 1984; Bouček 1988a). According to Graham (1969) 31 pteromalid genera belong to 11 subfamilies.

Default settings of PAUP (Phylogenetic Analysis Using Parsimonie. Version 3.1.1. Swofford 1993) were used for the cladistic analyses. The amount of data pretended the ‘heuristic tree search’ mode. MacClade 3.0 (Maddison & Maddison 1992) was used to view the offered character evolution. In the course of a first analysis all character states were given the same weight. Afterwards the *Successive Approximations Approach to Character Weighting* (Farris 1969) was used to reach a higher level of objectiveness.

The first analysis included 38 taxa. To reduce homoplasy effects, the number of examined taxa was decreased to 31. As a result seven taxa were excluded which had appeared in the same monophyletic clusters throughout all the analyses done so far.

Results

A first analysis containing all 38 taxa with equal character weights led to 8 shortest, most parsimonious trees with 700 steps. The consistency index (CI) is 0.254, respectively 0.251 without non-informative characters. After the third run of the *Successive Approximations Approach to Character Weighting* (Farris 1969), the resulting cladograms were stable, with CI=0.467 (0.445). *Dibrachys*, *Gastracanthus*, *Mesopolobus*, *Nasonia*, *Ormyrus*, *Pachycrepoideus*, *Perilampus*, *Pycnetron* and *Torymus* appeared in both cladograms in the same monophyletic clusters and were deleted for a second row of analyses. The analysis with equal character weights led to 2 shortest trees with 563 steps and a CI = 0.313 (0.306). After one run of the *Successive Approximations Approach to Character Weighting* (Farris 1969) the cladograms were stable with CI = 0.480 (0.441).

Discussion

The choice of *Eurytoma* and *Brachymeria* as outgroup taxa was supported in all analyses. This findings supports Bouček's (1988a) view that the Eurytomidae and the Chalcididae resemble rather primitive chalcids. In the analysis containing 38 taxa with all characters given the same weight, the possibly monophyletic groups *Eucharis* (Eucharitidae) and *Perilampus* (Perilampidae) on one hand and *Monodontomerus*, *Torymus* (both Torymidae) and *Ormyrus* (Ormyridae) on the other hand would render the family Pteromalidae polyphyletic (Fig. 1). After reweighting the characters, *Eucharis* + *Perilampus* appear as the most basal ingroup clade and would not render Pteromalidae + Torymidae + Ormyridae polyphyletic (Fig. 2). The analyses including 31 taxa indicate, too, that the Pteromalidae are an artificial assemblage rather than a monophyletic taxon (Figs 3, 4). *Spalangia* and *Asaphes*, representing the pteromalid subfamilies Spalangiinae and Asaphinae, appear in all analyses as the most basal pteromalid lineages. According to Bouček (1988b), the Spalangiinae are one of the more outstanding subfamilies, which may be "close to the Cerocephalinae". "The latter can be derived from Diparinae and these again from Cleonyminae" (Bouček 1988b). This view could not be supported by our analyses (Figs 1 to 4). *Cleonymus* (Cleonyminae) as well as the taxon here called cf. *Parurios* (Diparinae) seem to be more derived than *Spalangia* and *Asaphes* (Figs 1 to 4). Especially the more derived lineage here found for *Cleonymus* is in contrast with the view held by most chalcidologists who consider the Cleonyminae to be one of the oldest pteromalid lineages (Bouček 1958, 1988a). In cladistic analyses by Huang (1993) the Asaphinae also appeared as a basal branch of the Pteromalidae, which would support the results found here. *Eucharis* + *Perilampus* appear as monophyletic lineages in the analyses that included 38 taxa (Figs 1, 2), which would support Heraty & Darling (1984). It seems likely that the planidial larvae is a synapomorphy of Eucharitidae, Perilampidae and *Chrysolampus* (Heraty & Darling 1984). The results found here indicate a closer (Figs 1, 3 and 4) or a less close (Fig. 2) relationship of these taxa, but *Chrysolampus* appears just in one case as the sister-taxon of *Eucharis* (Fig. 4). The analyses with 38 taxa (Figs 1 and 2) suggest that *Ormyrus* + (*Torymus* + *Monodontomerus*) form a monophyletic lineage. A possible sister-group relationship of Ormyridae and Torymidae is widely discussed (Bouček 1988a; Grissell 1995), and the monophyly of the latter seems to be well supported, too (Grissell 1995; Gibson *et al.* 1999). This possibly monophyletic lineage seems to be an early branch in the Pteromalidae discussed here and would render Pteromalidae as a polyphyletic group (Figs 1 to 4). The position of *Panstenon* (Panstenoninae)

varies extremely throughout the analyses (Figs 1 to 4) and reflects the questionable relationship of this taxon (Bouček 1988a; Heydon 1997). A similar situation is found in the lineage *Trigonoderus* + *Gastracanthus* that appears to be monophyletic. Bouček (1998a) placed them in the tribe Trigonoderini in the Pteromalinae, whereas Graham (1969), placing them in the same tribe, assigned the tribe in the Miscogasterinae. Heydon (1997) reviewed the Trigonoderini genera of the world and their possible relationship and discussed the problems in the classification of this group. The results of our analyses (Figs 1 to 4) support the suggested close relationship with the Cleonyminae (Heydon 1997).

Graham (1969) considered the Pteromalinae to be the central subfamily of the Pteromalidae. While most of other pteromalid subfamilies are defined by special characters or combinations of characters, it is hard to come up with a formal definition of the Pteromalinae (Graham 1969). Bouček (1988a) refers to many unsolved taxonomical problems in this subfamily and suggests a classification different from the one that Graham (1969) has proposed. Our results underline these difficulties. While *Psilonotus* is found in quite a basal branch in the analyses including 38 taxa (Figs 1 and 2), it nevertheless seems to be closely related to other genera being regarded as Pteromalinae plus *Cleonymus* in the analyses with 31 taxa (Figs 3 and 4). The position of *Sphegigaster* and *Syntomopus* would support Bouček's (1988a) view that these two taxa belong to the tribe Pteromalini in the Pteromalinae, while Graham (1969) classified them in a tribe Sphegigasterini in the Miscogasterinae. Bouček (1988a) suggested a tribe Pteromalini, containing – apart from *Syntomopus* and *Sphegigaster* – *Dibrachys*, *Mesopolobus*, *Nasonia*, *Pachycrepoideus*, *Pachyneuron*, *Pteromalus* and *Pycnetron*. All these genera are classified in Bouček's (1988a) tribe Pteromalini and form along with *Arthrolytus*, obviously no member of the australasian fauna, a monophyletic taxon following our results (Figs 1 to 4). A monophyletic tribe Pteromalini would be contrary to other cladistic analyses (Huang 1993). The taxonomical position of *Sphaeripalpus* remains unclear and is unstable in our results (Figs 1 to 4). A relatively basal position to a cluster mainly formed by members of the Miscogasterinae and Pteromalinae *sensu* Graham (1969) is also found in cladistical analyses by Heydon (1988) and Huang (1993). Following the analyses with reweighted characters in particular (Figs 2 and 4) *Cratomus* (Cratominae) seems to be closely related to the genera mostly belonging to the Pteromalini *sensu* Bouček (1988a). Despite *Cratomus*' peculiar head the phenetical similarity with other taxa of the Pteromalini is obvious. As a consequence this suggests a deletion of the subfamily Cratominae.

Beside the Pteromalinae, according to Graham (1969), the Miscogasterinae form another central subfamily in the Pteromalidae. This taxon is questionable according to Bouček's (1988a) classification and the cladistic analyses of Huang (1993). Bouček (1988a) classified Graham's (1969) tribe Miscogasterini as a subfamily Miscogasterinae. The positions of typical Miscogasterinae-taxa *sensu* Graham (1969) like *Cyrtogaster*, *Halticoptera*, *Rhincocoelia*, *Sphaeripalpus* and *Thinodytes* are more or less variable in our cladograms (Figs 1 to 4), *Sphegigaster* and *Syntomopus* have been discussed above. This may underline the taxonomical problems of these taxa, which are also found in the cladistic analyses of Huang (1993) and the revision of the australasian fauna by Bouček (1988a). Although our results indicate a close relationship of *Gastrancistrus* and *Macroglenes* (Figs 1 to 4), they appear as sister-taxa in only one analysis (Fig. 4). A closer relationship of *Gastrancistrus* and *Ormocerus* suggested by Graham (1969) is not supported by our results. Graham (1969) classified both genera in the tribe Ormocerini in the subfamily Miscogasterinae. The rather basal position of *Ormocerus* (Figs 1 to 4) seems to be congruent with Bouček's (1988a) view who considers the Ormocerinae to be "rather primitive pteromalids".

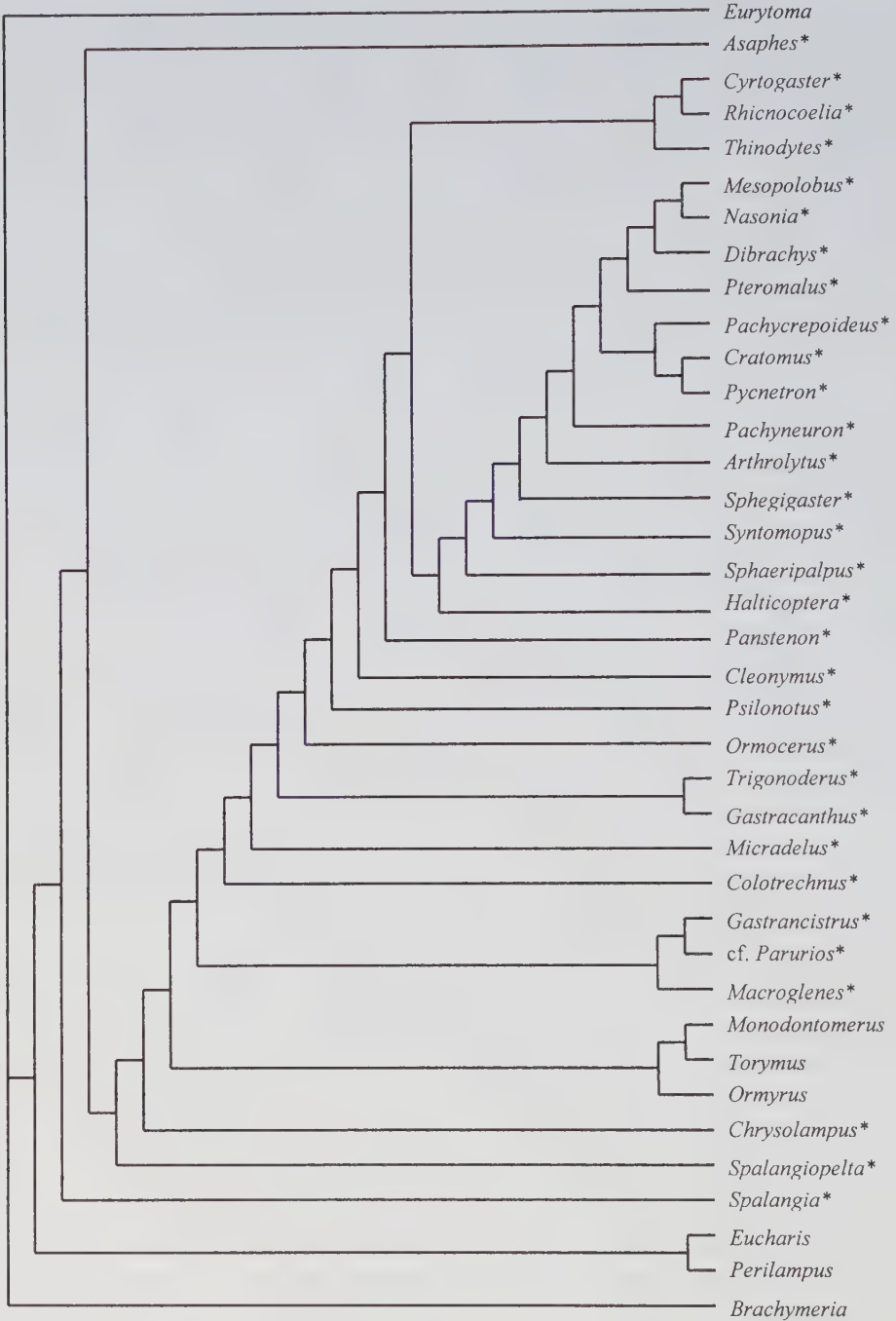


Figura 1 Strict consensus tree of eight most parsimonious trees with 38 taxa.
 Taxa marked with * belong to Pteromalidae (Noyes 1998)

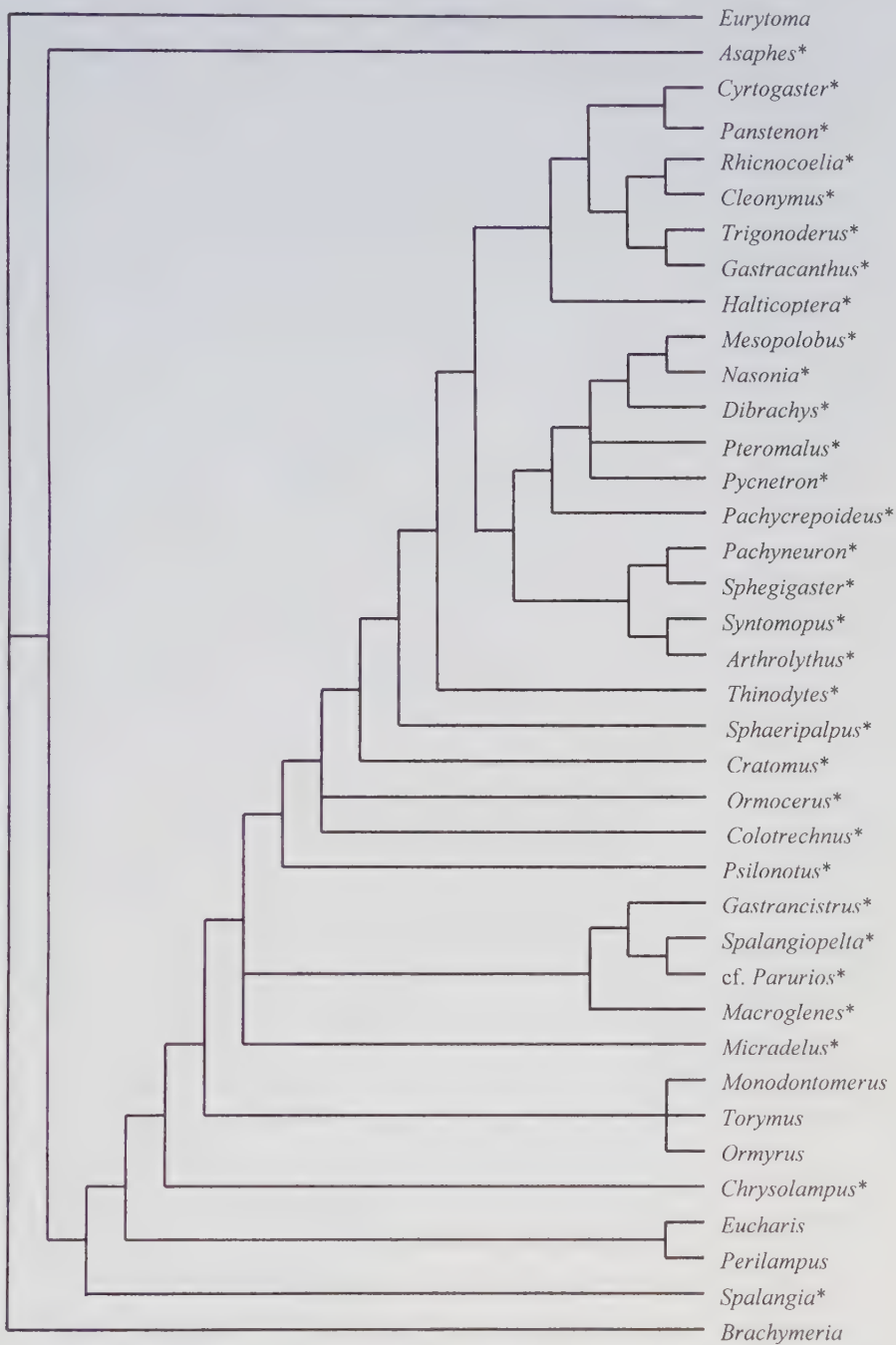


Figura 2 Reweighted tree with 38 taxa. Taxa marked with * belong to Pteromalidae (Noyes 1998)



Figura 3 Strict consensus tree of two most parsimonious trees with 31 taxa. Taxa marked with * belong to Pteromalidae (Noyes 1998)



Figura 4 Reweighted tree with 31 taxa. Taxa marked with * belong to Pteromalidae (Noyes 1998)

The position of *Micradelus* remains questionable. Graham (1969) classified this genus in the tribe Micradelini in the Miscogasterinae. A closer relationship of *Micradelus* to other Miscogasterina taxa *sensu* Graham (1969) is not likely (Figs 1 to 4).

The classification of the genera *Colotrechnus*, cf. *Parurios* and *Spalangiopelta* remains unclear. All of them appear in more or less basal branches, but without clear relationships to other taxa.

Although our results strikingly indicate that the Pteromalidae are polyphyletic, many questions still remain concerning the phylogeny of the Chalcidoidea. As a result the position of many of the investigated taxa is still unclear. Apart from this, the evolution of most characters remains questionable, too. Some of the characters and character states may not be useful for the whole group, but may help solve the situation in more terminal branches. It has been discussed (e.g. Heydon 1988) that character states, proved to be homoplastic along the whole tree, might be very helpful in other parts of the tree. Considering that it is difficult to find enough characters for cladistic analyses of such a large and highly diverse group, every character could lead to satisfying results in special branches of the tree.

Nevertheless, finding more and useful characters is a very important task. Beside molecular data (e.g. Downton & Austin 1994; Carpenter & Wheeler 1999), biological studies (e.g. Whitfield 1998) as well as comprehensive functional and morphological examinations, like the ones carried out by Gibson (1985) on thoracic structures of Hymenoptera or on complex morphological features of the Eupelmidae (Gibson 1989), and on mouthparts in Pteromalidae (Dzhanokmen 1996), may shed a new light on the still dimly lit evolutionary history of the Chalcidoidea. It is unavoidable to search for synapomorphies in order to define monophyletic groups and to find sister-group relationships. Along this line some more questionable and possibly ancient taxa should be included in further phylogenetic analyses.

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Appendix 1

Character and character states used in the cladistic analyses

Number of antennal segments: 13 (0); 12 (1); 11 (2); 10 or less (3).

Number of anelli: 0 (0); 1 (1); 2 (2); 3 or more (3).

Clava distinctly three-segmented (0); claval segments almost completely fused (1); clava two-segmented or absent (2).

Preclaval segment normal (0); with finger-like process (1).

Number of antennal segments equal in both sexes (0); unequal (1).

Number of anelli equal in both sexes (0); unequal (1).

Number of claval segments equal in both sexes (0); unequal (1).

Antennal setae in both sexes short, antennal segments more or less adjacent (0); males with long, distinctly projecting setae (1).

Funicular segments of similar shape in both sexes (0); funicular segments in males of distinctly different shape than in females (1).

Antennae in both sexes more or less clavate (0); in both sexes filiform (1); female antennae clavate, male antennae filiform (2).

Antennae in both sexes of relative same length (0); antennae in males distinctly longer than in females (1); antennae in females distinctly longer than in males (2).

Antennal insertion more or less mid-facial (0); near mouth margin (1); distinctly above middle of face (2); below middle of face, but distinctly distant to mouth margin (3).

Scrobes rather deep and completely carinate (0); scrobes deep, but incompletely carinate (1); scrobes slightly to not deepened (2).

Inner margin of eyes more or less parallel sided (0); slightly divergent (1); strongly divergent ventrally (2).

Surface of the face smooth and shiny (0); finely reticulated (1); densely punctured (2); ribbed (3); scaly (4).

Anterior tentorial pits deep (0); indistinct, but visible (1); invisible (2).

Clypeus distinctly separated from face and lying in a different plane (0); clypeus in the same plane than face, but with distinct epistomal sulcus (1); clypeus without epistomal sulcus, but with differently structured surface than the face (2); clypeus neither with epistomal sulcus, nor with different sculpture (3).

Anterior margin of clypeus straight to slightly concave (0); medially slightly incised (1); truncate (2); with single, median tooth (3); with two teeth, inbetween deeply incised (4); with three teeth (5).

Anterior clypeal margin symmetrical (0); asymmetrical (1).

Mandibles sickle-shaped, bidentate (0); relatively short, distal margin broad, bidentate (1); short, distally broadened, with three to four teeth (2); sickle-shaped, pointed (3).

Malar sulcus deepened throughout (0); indistinct, visible just in suitable light and angle (1); absent (2); rather carinated than deepened (3).

Occipital carina sharp at least below middle of eyes (0); sharp, but not reaching middle of the eyes (1); indistinct (2); absent (3).

Head more or less triangled (0); rounded (1); broad oval (2); longer than broad (3).

- Gena rounded (0); keeled (1).
- Ventral caput with hypostomal bridge (0); postgenal bridge (1).
- Hypostomal sulcus relatively short, dorsally more or less rectangular bended, hypostomal carinae weak (0); hypostomal sulcus relatively long, hypostomal carinae distinct, almost parallel, dorsally slightly converging (1); hypostomal sulcus relatively very short, sulci dorsally more or less regularly converging (2).
- Postoccipital carina absent (0); distinct (1).
- Hypostomal carina passing into postoccipital carina (0); hypostomal and postoccipital carinae more or less parallel, but not passing into each other (1); postoccipital carina extending latero-ventral, not connecteg with hypostomal carina (2).
- Stipes relatively short, more or less roundly swollen (0); stipes elongate, more or less parallel sided (1); stipes elongate, dorsally distinctly broader than ventral (1).
- Posterior tentorial pits dot-like (0); distinctly elongate (1).
- Collare of pronotum at least 1/3 the length of the mesoscutum (0); shorter (1).
- Anterior margin of pronotal collare without carina (0); with carina throughout (1); without sharp keel, but distinctly folded (2); with lateral carina, medially absent (3).
- Collare in dorsal view relatively long, anterior and posterior margin more or less parallel-sided (0); bell-shaped, medially distinctly longer than laterally (1); relatively short, more or less parallel-sided, medially at least as half as long as laterally (2); anterior margin more or less straight, posterior margin strongly concave, thought collare laterally at least two times as long as medially (3).
- Collum falls sharply or at a right angle with a pointing edge just before collare (0); Collum falls sharply before collare but edge is clearly rounded (1); no sharp fall and no edge between collare and collum (2).
- Neck of collum relatively short (0); extended (1).
- Pronotum laterally more or less quadratic, without impression (0); more or less quadratic, with distinct impression (1); distinctly shorter than high, without impression (2); distinctly shorther than high, with impression (3).
- Median mesoscutal line on mesoscutum absent (0); present (1).
- Notauli complete, deep throughout (0); complete, but indistinct (1); incomplete, at least posterior absent (2).
- Notauli and scutoscutellar sutures meeting at the transscutellar articulation, though seeming to pass into each other (0); posterior distance of notauli distinctly larger than anterior distance of scutoscutellar sutures (1); posterior distance of notauli distinctly smaller than anterior distance of scutoscutellar sutures (2).
- Transscutellar articulation more or less straight (0); distinctly curved, though anterior margin of axillae distinctly more anterior than anterior margin of the scutellum (1).
- Scutellum anterior with deepening (0); without deepening (1).
- Scutellum anterior distinctly deepend (0); without deepening, but anterior margin distinctly marched in (1); without deepening or marching in (2).
- Anterior margin of the scutellum straight (0); rounded (1).
- Frenum distinct (0); indistinct, but present (1); absent, sculpture of scutellum uniform throughout (2); absent, but sculpture of postnotum (?) different to that of the scutellum (3).
- Scutellum longer than broad (0); as long as or shorter as broad (1).

- Scutellum with rather dense, regularly short pilosity (0); rather sparsely, shortly pilose (1); in addition to more or less dense short pilosity with rather long, pairwise arranged setae (2); sparsely but long pilose (3); no pilosity (4).
- Scutellum in lateral view arched, overhanging dorsellum at least half the length of latter (0); scutellum arched, but not overhanging dorsellum (1); scutellum more or less flattened, without any process posterior (2); scutellum flattened, with posterior process (3).
- Width of axillae larger than the smallest distance of axillae (0); width of axillae equal or smaller than smallest distance of axillae, though axillae rather far apart from each other (1).
- Meso- and metacoxa inserted at about the same ventral-dorsal level (0); metacoxa distinctly more posterior inserted than mesocoxa (1); mesocoxa posterior to metacoxa inserted (2).
- Meso- and metacoxa inserted at about the same anterior-posterior level (0); metacoxa distinctly above level of mesocoxa inserted (1).
- Procoxa longer than metacoxa (0); procoxa about as long as metacoxa (factor 0.9 to 1.1) (1); metacoxa somewhat longer than procoxa (factor >1.1 to 1.5) (2); metacoxa more than 1.5 times longer than procoxa (3).
- Procoxa less than 1.5 times as long as broad (0); procoxa 1.5 to 2.5 times as long as broad (1); Procoxa more than 2.5 times as long as broad (2).
- Metacoxa less than 1.5 times as long as broad (0); metacoxa 1.5 to 2.5 times as long as broad (1); Metacoxa more than 2.5 times as long as broad (2).
- Mesocoxa less than 1.2 times as long as broad (0); mesocoxa 1.2 to 1.7 times as long as broad (1); Mesocoxa more than 1.7 times as long as broad (2).
- Mesepimeron with longitudinal rugae, not divided in upper and lower mesepimeron (0); mesepimeron smooth, not divided in upper and lower mesepimeron (1); upper mesepimeron smooth, lower reticulate (2); upper and lower mesepimeron reticulate, but distinctly differentiated (3); mesepimeron not divided in upper and lower mesepimeron, mainly smooth with fine punctures (4).
- Mesepimeron not differentiated or not divided in upper and lower mesepimeron (0); mesepimeron indistinctly divided in upper and lower mesepimeron, cross furrow incomplete (1); mesepimeron distinctly divided, cross furrow complete throughout (2).
- Mesepimeron without deepening (0); with indistinct puncture-like deepening (1); with distinctly puncture-like deepening (2); with distinct cross furrow, dividing mesepimeron in upper and lower epimeron (3).
- Mesopleuron distinctly divided in mesepimeron and mesepisternum, pleural sulcus distinct (0); mesopleuron distinctly divided in mesepimeron and mesepisternum, pleural sulcus indistinct (1); mesopleuron not differentiated in mesepimeron and mesepisternum (2).
- Metapleuron more or less rectangular and large (0); relatively small and more or less triangled (1); metapleuron relatively small, overlapped by mesopleuron (2).
- Prepecti ventral not fused (0); fused (1).
- Ventral fusion of prepecti articulated with mesosternum (0); grown together with mesosternum (1); grown together with pronotum (2).
- Prepectus not extending to base of procoxa (0); extending to base of procoxa (1).
- Prepectus relatively small (0); of medium size (1); relatively large (2); very small, almost invisible (3).
- Propodeum smooth (0); rugose (1); with differentiated nucha and/or plicae and/or median carina and/or costula.

- Propodeal stigmata situated close to anterior margin of propodeum (0); about in middle of propodeal length (1).
- Propodeal stigmata elongate-oval (0); more or less circular (1); elongate and kidney-shaped (2).
- Nucha present (0); absent (1).
- Median carina on propodeum absent (0); present (1); without median carina, but propodeum distinctly arched medially (2).
- Propodeal plicae absent (0); present (1).
- Propodeal costula absent (0); present (1).
- Propodeum rugose throughout (0); median area and calli reticulate (1); median area reticulate, calli smooth (2); propodeum smooth throughout (3); median area laterally smooth, calli and middle of propodeum crenulate (4).
- Both sexes macropter (0); females macropter, males brachypter (1).
- Basal vein unpigmented, without hairs (0); pigmented (1); unpigmented, but with a more or less complete row of setae (2).
- Basal cell bare (0); partly pilose (1); completely pilose (2).
- Postmarginal vein distinctly longer than marginal vein (0); postmarginal vein from half as long to about as long as marginal vein (1); postmarginal vein distinctly shorter than marginal vein (2).
- Stigmal vein very short (0); longer (1).
- Speculum absent (0); present, but small (1); distinct (2).
- Additional veins without rows of setae (0); with row of setae (1).
- Metafemur broad oval, toothed (0); slightly broadened, toothed (1); slightly broadened, without teeth (2); not broadened (3).
- Two metatibial spurs of equal length (0); two spurs of unequal length (1); one spur (2).
- Gaster sessil (0); petiolus visible, but broader than long (1); petiolus at least as long as broad (2).
- Gastral tergites 7 and 8 (T7, T8) fused to epipygium (0); T7 and T8 not fused, T7 dorsally more or less parallel sided, sometimes posteriorly divided, T8 fingernail-like, through membrane distinctly divided from T8 (1).
- Cerci long (0); cerci short, plate-like (1).
- Ovipositor at tip of gaster distinctly protruding (0); not to slightly protruding (1); ovipositor distinctly protruding ventrally at about half length of gaster (2).
- No planidial larvae (0); planidial larvae (1).
- Phytophagous (0); parasitoids of gall-inducing insects, miners or stem-borers (1); solitary parasitoids of exposed hosts (2); gregarious (3); associated with wood-boring insects (4); parasitoids in ants' nests (5).
- Mesoscutal surface punctate, with hairs (0); net-like structure with creases (1); alutaceous (2); reticulate (3); smooth (4); striate (5).
- Reticulation elevated (0); engraved (1).
- Pilosity: one hair per puncture (0); dense pilosity on scale-like surface (1); hairs on smooth surfaces surrounding net-like structures (2); pilosity on papillae (3); surface smooth, without pilosity (4).
- Without metallic luster, brown or black animals (0); with metallic luster (1).

Appendix 2

#NEXUS

begin data;

dimensions ntax=38 nchar=90;

format symbols="012345";

matrix

Asaphes	01010 00000 00110 00000 00010 11211 00010 30000 00000 22001 02001 02211 01120 11101 00210 11132 20110 22?31
Cyrtogaster	02030 00000 00111 11502 12201 11121 11301 20110 11121 22001 20002 11111 01110 11010 00211 12132 20110 13021
Eurytoma	11100 00011 10002 23101 33011 01211 00001 20000 00020 01100 12110 00101 11110 11?00 00211 12121 10110 ?0?00
Gastrancistrus	21030 00111 2?114 13002 13201 11101 10200 20000 12010 22001 31113 11011 01200 10000 30202 12122 00120 13121
Mesopolobus	02030 00000 0?211 21202 12101 10111 11200 30211 12010 22101 31112 11111 01120 01110 20001 12132 00110 13021
Monodontomer	01030 00000 00104 23002 00201 01101 00011 20011 00001 00011 31101 02111 01120 2?101 ?0212 02111 01000 ?1?11
Nasonia	02030 00000 00214 11202 12200 10110 10200 30211 11110 12101 21102 11111 01120 01110 11001 12032 00110 33121
Pachycrepoide	03030 00000 00111 22202 13110 1101? 00001 30200 11031 12101 21013 01111 00220 01210 10200 12132 20110 23021
Pachyneuron	02000 00011 21111 22202 13210 1101? 11200 30211 11131 12001 21112 11111 01120 01010 20000 12132 20110 33021
Pteromalus	02000 00010 ?1211 22202 13100 10111 10200 30201 12031 11101 21102 11111 01110 01110 20001 12132 00110 ?3021
Rhinochoelia	02030 00011 21201 21512 0320? ???1? 10301 00111 12010 22001 20012 11111 01120 11210 00211 12131 10110 ?3021
Spalangia	10110 00?01 01212 20?0? 003?? 21101 00121 00010 00101 02001 12101 11101 112?0 11110 40002 02132 20010 20?01
Sphegigaster	02000 00001 21211 22402 23100 1112? 11301 302?1 11120 12001 11102 11111 01220 01000 20201 12132 20110 13021
Syntomopus	02030 00001 01211 21502 23100 1101? 01201 10110 11111 42010 11012 11111 01220 01110 20211 12132 20110 13021
Thinodytes	02030 00000 00211 21412 2320? ???1? 10201 30111 11121 21001 20102 11111 00120 01110 30201 12132 20110 ?3021
Torymus	01130 00000 00111 13002 00001 01101 10221 ?0011 12020 03011 31011 23011 01100 00000 30212 01132 00010 11?11
Brachymeria	01030 00000 00012 10001 33011 01?20 13200 20000 00021 00111 31100 00000 ??310 21200 00102 01102 10110 ?0?00
Ormyrus	02030 00000 00101 10002 10101 01101 00010 ?0111 12020 ?0101 31121 00011 000?0 00200 10202 02121 01110 11?31

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Spalangiopelta 03010 001?? 1?111 13000 1310? 1??1? 10221 10000 12001 22101 1212? ?0?21
112?1 10200 10101 10032 10100 ?1?31
Chrysolampus 01030 000?? 0?113 11000 0311? 1??1? 01201 10010 11120 30000 20111 03011
01220 00100 10002 02132 20?11 ?1?31
Panstenon 02000 00000 10201 21002 02110 1??1? 11121 102?1 11100 22010 20103 10011
01220 11000 00221 10132 20000 13021
Trigonoderus 02030 00001 11114 0130? 0320? 1012? 11321 00011 ??101 02001 22222 11011
01220 00110 10120 1013? 00110 43021
Gastracanthus 02000 00011 11114 0120? 03201 1??21 10321 00010 11100 22001 20112 23011
01220 10110 10110 12132 10?10 ?3021
Halticoptera 02030 00000 00211 21412 03200 1??21 10021 102?1 11121 41001 21012 11111
01220 11110 10211 12132 20110 13021
Sphaeripalpus 02030 00000 21211 21402 0320? 1??1? 10201 20111 11110 41001 11102 23011
01220 01000 10211 12132 20110 ?3021
Micradelus 13030 00000 00121 11200 1310? 1??1? 10200 20011 12020 02021 22111 01011
01120 10200 10120 10132 10?10 ?3??0
Ormocerus 02000 00000 00111 21402 0310? 1??1? 10201 30011 12020 21011 21002 23011
01220 10100 10001 12122 10120 13??1
Macroglenes 33010 01000 00210 2300? 2110? 1??1? 10001 20020 12001 22101 21111 13011
01220 10200 30012 02132 00000 13121
Cratomus 00030 00000 00001 2220? 2320? 1101? 10201 30201 12020 11001 11102 2301?
?0020 01200 1?221 11132 201?0 ?3020
Colotrechnus 02030 1??1? ??114 23002 0?10? 1??1? 10200 ?02?? 12021 20101 211?? 1??1?
?1?20 10100 00002 0202? 00?10 13021
Cleonymus 01011 01?11 02221 12001 03200 0?11? 0001? 102?1 12021 02010 30012 11111
?1220 00100 20221 10111 10110 43021
cf. Parurios 01010 00111 11103 23302 00111 0?120 10201 30000 12001 22001 31201 10111
00110 01100 00111 10131 10000 ?5?21
Pycnetron 03000 010?? ??011 22202 1321? 1??1? 10200 30101 ?2031 10101 21012 23111
?0120 01111 3?101 12121 00110 43021
Arthrolytus 02010 00111 11211 22202 13100 11011 1220? 10201 11010 22000 11012 21011
01220 01111 10201 12132 00110 13021
Psilonotus 03010 000?? 11211 11402 0310? 1101? 11300 102?1 12021 22110 2101? ?2011
01220 00100 30001 12122 00110 13121
Eucharis 30100 1??1? ??101 01203 2120? 1??1? ?0?00 210?0 11121 40010 20004 10100
20220 11000 10002 0??30 20?11 54?41
Perilampus 01000 00000 00101 21003 00100 1101? 11200 210?0 11121 00000 20000 21101
21210 21111 ?0001 10130 10?11 20?01
Dibrachys 02030 00000 10201 21202 12100 1011? 12201 30200 12031 22101 20002 11111
01120 01110 10001 12132 10110 33021
;end;

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Appendix 3 Table 1 Data matrix, characters 1–30.

Character/ Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Asaphes	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	2	1	1
Cyrtogaster	0	2	0	0	0	0	0	0	0	0	0	3	1	1	1	1	1	5	0	2	1	2	2	0	1	1	1	1	2	1
Eurytoma	1	1	1	0	0	0	0	1	1	1	0	0	0	0	2	2	3	1	0	1	3	3	0	1	1	0	1	2	1	1
Gastrancistrus	2	1	0	0	0	0	1	1	1	2	?	3	1	1	4	1	3	0	0	2	1	3	2	0	1	1	1	1	0	1
Mesopobolus	0	2	0	0	0	0	0	0	0	?	?	3	2	1	1	2	1	2	0	2	1	2	1	0	1	1	0	1	1	1
Monodontomerus	0	1	0	0	0	0	0	0	0	0	0	3	1	0	4	2	3	0	0	2	0	2	0	1	0	1	1	0	1	0
Nasonia	0	2	0	0	0	0	0	0	0	0	0	3	2	1	4	1	1	2	0	2	1	2	2	0	0	1	0	1	1	0
Pachycrepoides	0	3	0	0	0	0	0	0	0	0	3	1	1	1	1	2	2	2	0	2	1	3	1	1	0	1	1	0	1	?
Pachyneuron	0	2	0	0	0	0	1	1	2	1	0	2	1	1	1	2	2	2	0	2	1	3	2	1	0	1	1	0	1	?
Pteromalus	0	2	0	0	0	0	0	1	0	?	1	0	2	1	1	2	2	2	0	2	1	3	1	0	0	1	0	1	1	1
Rhincocoeila	0	2	0	0	0	0	0	1	1	2	1	3	2	0	1	2	1	5	1	2	0	3	2	0	?	?	?	?	1	?
Spalangia	1	0	1	0	0	?	0	1	0	1	1	2	1	1	2	2	0	?	0	?	0	3	?	?	?	2	1	1	0	1
Sphegigaster	0	2	0	0	0	0	0	0	1	2	1	0	2	1	1	2	2	4	0	2	2	3	1	0	0	1	1	1	2	?
Syntomopus	0	2	0	0	0	0	0	1	0	1	3	2	1	1	2	1	5	0	2	2	3	1	0	0	1	1	0	1	?	?
Thiridocyttus	0	2	0	0	0	0	0	0	0	0	3	2	1	1	2	1	4	1	2	2	3	2	0	?	?	?	?	?	1	?
Torymus	0	1	1	0	0	0	0	0	0	0	0	3	1	1	1	1	3	0	0	2	0	0	0	0	1	0	1	1	?	0
Brachymeria	0	1	0	0	0	0	0	0	0	0	0	3	1	1	2	1	0	0	0	1	3	3	0	1	1	0	1	?	2	0
Ormyrus	0	2	0	0	0	0	0	0	0	0	0	3	1	0	1	1	0	0	0	2	1	0	1	0	1	0	1	1	0	1
Spalangioipelta	0	3	0	0	0	0	1	?	?	?	1	1	1	1	1	1	3	0	0	0	1	3	1	0	?	?	?	?	?	?
Chrysolampus	0	1	0	0	0	0	?	?	?	?	?	3	1	1	3	1	1	0	0	0	0	3	1	1	?	?	?	?	?	?
Panstenon	0	2	0	0	0	0	0	0	0	1	0	0	2	0	1	2	1	0	0	2	0	2	1	1	0	1	?	?	?	?
Trigonoderus	0	2	0	0	0	0	0	1	1	1	1	3	1	1	4	0	1	3	0	?	0	3	2	0	?	?	1	0	1	?
Gastrancanthus	0	2	0	0	0	0	1	1	1	1	1	0	1	1	4	0	1	2	0	?	0	3	2	0	1	1	?	?	?	?
Halictoptera	0	2	0	0	0	0	0	0	0	0	0	3	2	1	1	2	1	4	1	2	0	3	2	0	0	1	?	?	?	?
Sphaerpalpus	0	2	0	0	0	0	0	0	0	2	1	3	2	1	1	2	1	4	0	2	0	3	2	0	?	?	?	?	?	?
Micradelus	1	3	0	0	0	0	0	0	0	0	3	1	2	1	1	1	2	0	1	4	0	1	3	1	0	?	?	?	?	?
Ormocerus	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	2	1	4	0	2	0	3	1	0	?	?	?	?	?	?
Macroglenes	3	3	0	0	0	0	0	0	0	0	0	0	1	1	1	2	1	4	0	2	0	3	1	0	?	?	?	?	?	?
Cratomus	0	0	0	0	0	0	0	0	0	0	3	0	0	1	2	2	2	0	0	?	2	3	2	0	?	?	?	?	?	?
Colitrechus	0	2	0	0	?	?	?	?	?	?	?	3	1	1	4	2	3	0	0	2	0	?	1	0	?	?	?	?	?	?
Cleonymus	0	1	0	1	0	1	?	1	1	0	2	1	2	2	1	1	2	0	0	1	0	3	2	0	0	?	?	?	?	?
cf. Paruros	0	1	0	0	0	0	1	1	1	1	1	1	1	0	3	2	3	3	0	2	0	0	1	1	1	0	?	?	?	?
Pycnethon	0	3	0	0	0	0	1	0	?	?	?	?	0	1	1	2	2	2	0	2	1	3	2	1	?	?	?	?	?	?
Arthrolytus	0	2	0	0	0	0	1	1	1	1	1	1	2	1	1	2	2	2	0	2	1	3	1	0	0	1	1	0	1	1
Psilonotus	0	3	0	0	0	0	?	?	?	?	?	1	1	1	1	1	1	4	0	2	0	3	1	0	?	?	?	?	?	?
Eucharis	3	0	1	0	?	?	?	?	?	?	?	0	1	0	1	0	1	2	0	3	2	1	2	0	?	?	?	?	?	?
Perilampus	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2	1	0	0	3	0	0	1	0	0	1	1	0	?
Dibrachys	0	2	0	0	0	0	0	0	0	1	0	3	2	0	1	2	1	2	0	2	1	2	1	0	0	1	0	1	1	?

Table 1 (continued): data matrix, characters 31–60

Character/ Taxon	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	
<i>Asaphes</i>	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	2	2	0	0	1	0	2	0	0	1	0	2	2	1	2	
<i>Cyrtogaster</i>	1	1	3	0	1	2	0	1	1	0	1	1	1	2	1	2	2	0	0	1	2	0	0	0	2	1	1	1	1	2	
<i>Eurytoma</i>	0	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	1	1	0	0	1	2	1	1	0	0	1	1	0	2	
<i>Gastrancistrus</i>	1	0	2	0	0	2	0	0	1	2	0	1	2	0	1	0	2	2	0	0	1	3	1	1	3	1	1	0	1	2	
<i>Mesopolobus</i>	1	1	2	0	0	3	0	2	1	1	1	2	0	1	0	2	2	1	0	1	3	1	1	1	2	1	1	1	1	2	
<i>Monodontomerus</i>	0	0	0	1	1	2	0	0	1	1	0	0	0	0	1	0	0	0	1	1	3	1	1	1	1	0	2	1	1	2	
<i>Nasonia</i>	1	0	2	0	0	3	0	2	1	1	1	1	1	1	1	0	1	2	1	0	1	2	1	1	0	2	1	1	1	2	
<i>Pachycrepoides</i>	0	0	0	0	1	3	0	2	0	0	1	1	0	3	1	1	2	1	0	1	2	1	0	1	3	0	1	1	1	2	
<i>Pachyneuron</i>	1	1	2	0	0	3	0	2	1	1	1	1	1	3	1	1	2	0	0	1	2	1	1	1	2	1	1	1	1	2	
<i>Pteromalus</i>	1	0	2	0	0	3	0	2	0	1	1	2	0	3	1	1	1	1	0	1	2	1	1	1	0	2	1	1	1	2	
<i>Rhinochoelia</i>	1	0	3	0	1	0	0	1	1	1	1	2	0	1	0	2	2	0	0	1	2	0	0	1	2	1	1	1	1	2	
<i>Spalangia</i>	0	0	1	2	1	0	0	0	1	1	0	0	1	0	1	0	2	0	0	1	1	2	1	0	1	1	1	1	0	2	
<i>Sphegigaster</i>	1	1	3	0	1	3	0	2	?	1	1	1	1	2	0	1	2	0	0	1	1	1	1	1	0	2	1	1	1	2	
<i>Syntomopus</i>	0	1	2	0	1	1	0	1	1	1	0	1	1	1	1	1	4	2	0	1	0	1	0	1	0	2	1	1	1	2	
<i>Thinodytus</i>	1	0	2	0	1	3	0	1	1	1	1	1	1	2	1	2	1	0	0	1	2	0	1	0	2	1	1	1	1	2	
<i>Torymus</i>	1	0	2	2	1	?	?	?	0	0	1	1	2	0	2	0	0	3	0	1	1	3	1	0	1	1	2	3	0	1	2
<i>Brachymeria</i>	1	3	2	0	0	2	0	0	0	0	0	0	0	2	1	0	0	1	1	1	3	1	1	1	0	0	0	0	0	0	
<i>Ormyrus</i>	0	0	0	1	0	?	0	1	1	1	1	2	0	2	0	?	0	1	0	1	1	3	1	1	0	0	0	1	2		
<i>Spalangiopeila</i>	1	0	2	2	1	1	0	0	0	1	0	1	2	0	0	1	2	2	1	0	1	1	2	1	2	?	?	?	?	2	2
<i>Chrysolampus</i>	0	1	2	0	1	1	0	0	1	0	1	1	2	0	1	2	0	0	0	0	2	0	1	1	1	0	3	0	1	2	
<i>Panstenon</i>	1	1	1	2	1	1	0	2	?	1	1	1	1	0	0	2	2	0	1	0	2	0	1	0	3	1	0	0	1	2	
<i>Trigonoderus</i>	1	1	3	2	1	0	0	0	1	1	?	?	1	0	1	0	2	0	0	1	2	2	2	2	1	1	0	1	2		
<i>Gasiracanthus</i>	1	0	3	2	1	0	0	0	1	0	1	1	1	0	0	2	2	0	0	1	2	0	1	1	2	2	3	0	1	2	
<i>Halticoptera</i>	1	0	0	2	1	1	0	2	?	1	1	1	1	2	1	4	1	0	0	1	2	1	0	1	2	1	1	1	1	2	
<i>Sphaeripalpus</i>	1	0	2	0	1	2	0	1	1	1	1	1	1	1	0	4	1	0	0	1	1	1	1	0	2	2	3	0	1	2	
<i>Micradellus</i>	1	0	2	0	0	2	0	0	1	1	1	2	0	2	0	0	2	0	2	1	2	2	1	1	1	0	1	0	1	2	
<i>Ormocerus</i>	1	0	2	0	1	3	0	0	1	1	1	2	0	2	0	2	1	0	1	1	2	1	0	0	2	2	3	0	1	2	
<i>Macroglenes</i>	1	0	0	0	1	2	0	0	2	0	1	2	0	0	1	2	2	1	0	1	2	1	1	1	1	3	0	1	2		
<i>Criatomus</i>	1	0	2	0	1	3	0	2	0	1	1	2	0	2	0	1	1	0	0	1	1	1	1	1	0	2	3	0	1	?	
<i>Colotrechnus</i>	1	0	2	0	0	?	?	?	?	?	1	2	0	2	1	2	0	1	0	1	2	1	1	?	?	?	?	?	?	?	
<i>Cleonymus</i>	0	0	0	1	?	1	0	2	?	1	1	2	0	2	1	0	2	0	1	0	3	0	0	1	2	1	1	1	1	2	
<i>cf. Parusios</i>	1	0	2	0	1	3	0	0	0	1	2	0	0	1	2	2	0	0	1	1	3	1	2	0	1	1	1	0	1	2	
<i>Pycnetron</i>	1	0	2	0	0	3	0	1	0	1	?	2	0	3	1	1	0	1	0	1	2	1	0	1	2	2	3	1	1	2	
<i>Arthrolytus</i>	1	2	2	0	0	?	1	0	2	?	1	1	0	1	0	2	2	0	0	0	1	2	1	0	1	2	3	1	1	2	
<i>Psilonotus</i>	1	1	3	0	0	1	0	2	?	1	1	2	0	2	1	4	0	0	1	0	2	1	0	1	2	?	?	0	1	2	
<i>Eucharis</i>	?	0	?	0	0	2	1	0	?	0	1	1	1	2	1	4	0	0	0	0	2	0	0	0	4	1	0	1	0	1	
<i>Penlampus</i>	1	1	2	0	0	2	1	0	?	0	1	1	1	2	1	0	0	0	1	0	2	0	0	0	0	2	1	1	0	2	
<i>Dibrachys</i>	1	2	2	0	1	3	0	2	0	0	1	2	0	3	1	2	2	1	0	1	2	0	0	0	2	1	1	1	1	2	

Table 1 (continued): data matrix, characters 61–90

Character/ Taxon	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	
<i>Asaphes</i>	0	1	1	2	0	1	1	1	0	1	0	0	2	1	0	1	1	1	3	2	2	0	1	1	0	2	2	?	3	1	
<i>Cyrtogaster</i>	0	1	1	1	0	1	1	0	1	0	0	0	2	1	1	1	2	1	3	2	2	0	1	1	0	1	3	0	2	1	
<i>Eurytoma</i>	?	1	1	1	0	1	1	?	0	0	0	0	2	1	1	1	2	1	2	1	1	0	1	1	0	?	0	?	0	0	
<i>Gastrancistrus</i>	0	1	2	0	0	1	0	0	0	0	3	0	2	0	2	1	2	1	2	2	0	0	1	2	0	1	3	1	2	1	
<i>Mesopolobus</i>	0	1	1	2	0	0	1	1	1	0	2	0	0	0	1	1	2	1	3	2	0	0	1	1	0	1	3	0	2	1	
<i>Monodontomerus</i>	0	1	1	2	0	2	?	1	0	1	?	0	2	1	2	0	2	1	1	1	0	1	0	0	?	1	?	1	1	1	
<i>Nasonia</i>	0	1	1	2	0	0	1	1	1	0	1	1	0	0	1	1	2	0	3	2	0	0	1	1	0	3	3	1	2	1	
<i>Pachycrepoides</i>	0	0	2	2	0	0	1	2	1	0	1	0	2	0	0	1	2	1	3	2	2	0	1	1	0	2	3	0	2	1	
<i>Pachyneuron</i>	0	1	1	2	0	0	1	0	1	0	2	0	0	0	0	1	2	1	3	2	2	0	1	1	0	3	3	0	2	1	
<i>Pteromalus</i>	0	1	1	1	0	0	1	1	1	0	2	0	0	0	1	1	2	1	3	2	0	0	1	1	0	?	?	3	0	2	1
<i>Rhinochoelia</i>	0	1	1	2	0	1	1	2	1	1	0	0	2	1	1	1	2	1	3	1	1	0	1	1	0	?	3	0	2	1	
<i>Spalangia</i>	1	1	2	?	0	1	1	1	1	0	4	0	0	2	0	2	0	2	1	3	2	2	0	0	1	0	2	0	?	1	
<i>Sphegigaster</i>	0	1	2	2	0	0	1	0	0	0	2	0	2	0	1	1	2	1	3	2	2	0	1	1	0	1	3	0	2	1	
<i>Syntomopus</i>	0	1	2	2	0	0	1	1	1	0	2	0	2	0	1	1	2	1	3	2	2	0	1	1	0	1	3	0	2	1	
<i>Thinodius</i>	0	0	1	2	0	0	1	1	1	0	3	0	2	0	1	1	2	1	3	2	2	0	1	1	0	?	3	0	2	1	
<i>Torymus</i>	0	1	1	0	0	0	0	0	0	0	3	0	2	1	2	0	1	1	3	2	0	0	0	0	1	0	1	?	1	1	
<i>Brachymeria</i>	?	?	3	1	0	2	1	2	0	0	0	0	1	0	2	0	1	1	0	2	1	0	1	1	0	?	0	?	0	0	1
<i>Ormyrus</i>	0	0	0	?	0	0	0	2	0	0	1	0	2	0	2	0	2	1	0	2	1	0	1	1	0	1	1	?	3	1	
<i>Spalangiopepla</i>	1	1	2	?	?	1	1	0	2	0	0	1	0	1	0	1	0	0	3	2	1	0	1	0	0	?	1	?	?	3	1
<i>Chrysolampus</i>	0	1	2	2	0	0	0	1	0	0	1	0	0	0	2	0	2	1	3	2	2	0	?	1	1	?	1	?	?	3	1
<i>Parstenon</i>	0	1	2	2	0	1	1	0	0	0	0	0	2	2	1	1	0	1	3	2	2	0	0	0	0	1	3	0	2	1	
<i>Trigonoderus</i>	0	1	2	2	0	0	0	1	1	0	1	0	1	2	0	1	0	1	3	?	0	0	1	1	0	4	3	0	2	1	
<i>Gastrancanthus</i>	0	1	2	2	0	1	0	1	1	0	1	0	1	1	0	1	2	1	3	0	1	0	?	1	0	?	3	0	2	1	
<i>Halticoptera</i>	0	1	2	2	0	1	1	1	1	0	1	0	2	1	1	1	2	1	3	2	2	0	1	1	0	1	3	0	2	1	
<i>Sphaeripalpus</i>	0	1	2	2	0	0	1	0	0	0	1	0	2	1	1	1	2	1	3	2	2	0	1	1	0	1	3	0	2	1	
<i>Microdelus</i>	0	1	1	2	0	1	0	2	0	0	1	0	1	2	0	1	0	1	3	2	1	0	?	1	0	?	3	0	2	1	
<i>Ormocerius</i>	0	1	2	2	0	1	0	1	0	0	1	0	0	0	1	1	2	1	2	2	1	0	1	2	0	1	3	?	?	1	
<i>Macroglenes</i>	0	1	2	2	0	1	0	2	0	0	3	0	0	1	2	0	2	1	3	2	0	0	0	0	0	1	3	?	?	1	
<i>Cratimus</i>	?	0	0	2	0	0	1	2	0	0	1	?	2	2	1	1	1	1	3	2	2	0	1	?	0	?	3	1	2	1	
<i>Colarechnus</i>	?	1	?	2	0	1	0	1	0	0	0	0	0	2	0	2	0	2	0	2	?	0	?	1	0	1	3	0	2	2	
<i>Cleonymus</i>	?	1	2	2	0	0	0	1	0	0	2	0	2	2	1	1	0	1	1	1	1	0	1	1	0	4	3	0	2	1	
cf. <i>Parvius</i>	0	0	1	1	0	0	1	1	0	0	0	0	1	1	1	1	0	1	3	1	1	0	0	0	0	?	5	?	?	2	1
<i>Pycnetron</i>	?	0	1	2	0	0	1	1	1	1	3	?	1	0	1	1	2	1	2	1	0	0	1	1	0	4	3	0	2	1	
<i>Arthrolytus</i>	0	1	2	2	0	0	1	1	1	1	1	0	2	0	1	1	2	1	3	2	0	0	1	1	0	1	3	0	2	1	
<i>Psilonotus</i>	0	1	2	2	0	0	0	1	0	0	3	0	0	0	1	1	2	1	2	1	2	0	0	1	1	0	1	3	1	2	1
<i>Eucharis</i>	2	0	2	2	0	1	1	0	0	0	1	0	0	0	2	0	?	?	3	0	2	0	?	1	1	5	4	?	4	1	
<i>Perilampus</i>	2	1	2	1	0	2	1	1	1	1	?	0	0	0	1	1	0	1	3	0	1	0	?	1	1	2	0	?	0	1	
<i>Dibrachys</i>	0	1	1	2	0	0	1	1	1	0	1	0	0	0	1	1	2	1	3	0	1	0	1	1	0	3	3	0	2	1	

THE POWER OF MULTIVARIATE STATISTICAL METHODS IN THE TAXONOMY OF PTEROMALIDAE (HYMENOPTERA: CHALCIDOIDEA)

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Abstract – The present paper illustrates the use of multivariate statistical methods for separating species in Pteromalidae (Hymenoptera). Linear discriminant (DA) and principal components analysis (PCA) are applied to polythetic species of the *Pteromalus albipennis* group, i.e. to *P. albipennis*, *P. decipiens*, and *P. solidaginis*. A DA including 22 characters reveals clear gaps among those species and eliminates redundant characters. With PCA *P. solidaginis* differs from the other species by its shape or shape and size, whereas *P. decipiens* is separated from *P. albipennis* mainly by its smaller size. Possible implications of the results are discussed with regard to the status of the taxa.

Key words: principal components, linear discriminant functions, multivariate statistics, taxonomy, *Pteromalus*

Introduction

In Pteromalidae complexes of polythetic species are frequently encountered. This situation poses difficulties for the taxonomist, since such species cannot be separated by a single diagnostic character. Nevertheless, there is often apparent variation in proportions of many characters. Multivariate statistical methods could therefore be used to examine the variation in these structures and to uncover hidden differences between taxa. Studies that make explicit use of such statistical methods are rather rare in the taxonomic literature on Pteromalidae. Janzon (1986) investigating a subgroup of the *Pteromalus albipennis* species-group pointed out the effect of allometry on ratios used in taxonomy. However, the data were explored in a bivariate context, multivariate statistical methods were not applied.

The *Pteromalus albipennis* species-group was erected by Graham (1969) who included 23 Western European species. The group is certainly more widely distributed, since numerous species are known to the author from the Nearctic region (Baur, *unpubl.*). There is strong evidence that most species are parasitoids of fruit flies (Diptera: Tephritidae) on Asteraceae (Graham 1969; Janzon 1984; Baur, *unpubl.*). Despite investigations by Graham (1969) and Janzon (1984, 1986) on the *Pteromalus albipennis* species-group, there are still many unresolved problems. One of them concerns *P. solidaginis* Graham & Gijswijt 1991 (*sol*) and the very similar *P. albipennis* Walker, 1835 (*alb*) and *P. decipiens* Graham, 1969 (*dec*). Graham (1969) and Graham & Gijswijt (1991) mentioned qualitative characters, such as the colour of the flagellum, the veins and the body, but also certain ratios for the separation of these species. A re-examination of the type series and further material revealed that these characters were not reliable for a significant part of the material. Colour characters are difficult to interpret and some of the ratios showed considerable overlap between species. In an attempt to find additional evidence for separating these species, they were included in a multivariate morphometric analysis.

Materials and Methods

The study is based on an analysis of 66 dry mounted females (Appendix). These had to be assigned to a species before the analysis. Specimens of *alb* and *dec* were identified according to Graham (1969: 502) and compared with the lectotype (*alb*) or with paratypes (*dec*). For *sol* only paratypes were available. Individual specimens were provided with an identification label and a number to assure unambiguous recognition. Terminology and morphology follow Gibson (1997). 22 characters were selected for the analysis (Table 1). Measurements were made under a Leica MZ12 stereo-microscope with different magnifications using a calibrated eye-piece micrometer (12 mm subdivided into 120 units) (Table 1). To avoid additional variability resulting from possible fluctuating asymmetry, only the left hand side of a specimen was considered.

The morphometric analysis of the data followed a two-step procedure. A first step served to find the best separation between taxa (e.g. between *sol* and the other two species) and to identify redundant characters. Here, a linear discriminant analysis (DA) was the most appropriate method. In a second step the nature of the differences (e.g. size or shape differences) found with the reduced data set was investigated using a principal components analysis (PCA). The DA, as used here, is based on multiple regression and its application is discussed in detail by Flury & Riedwyl (1988). The procedure requires an additional code variable for the taxa which is treated as the dependent variable of the analysis. Thus an arbitrary number ("0" and "1") was assigned to each group. The characters, on the other hand, are considered the independent variables of the regression analysis. In an iterative process, redundant characters are identified and eliminated: First, a regression analysis including all independent variables (characters) is computed. Second, the variable showing the highest probability of F, i.e. contributing the least to the separation of taxa, is removed and a new regression analysis is run on the reduced data set. These steps are repeated until the probability of F is < 0.1 for the remaining variables. This so-called backward elimination method is fully implemented in the SPSS statistical software package. Thus, the best characters for separating the taxa can be identified very effectively. Finally, a PCA computed with this set of characters further reduces the dimensionality in the data and illuminates the nature of the differences between taxa. The PCA presented below was carried out on a correlation matrix. For further details concerning the computation and interpretation of this fundamental ordination technique I refer to Flury & Riedwyl (1988), Pimentel (1992), Manly (1994), and Podani (2000). Calculation of DA, PCA and the statistics presented below was done with SPSS for Windows (Release 11.0, SPSS Inc., 2001).

Results

Median and range of each character and species are given in table 1. From these Figures eight ratios, commonly used in pteromalid taxonomy (Graham 1969; Bouček 1988), were calculated (Fig. 1). These ratios show that *sol* is well separated from the two other species using POL/OOL and gaster L/B. Clearly, the ranges of several other ratios overlap, e.g. of eye H/B and propodeum L/B. Generally, *sol* seems to be closer to *dec*. On the other hand, *dec* and *alb* cannot really be diagnosed by any of those ratios, despite the fact, that sometimes statistically significant differences may occur (e.g. in head B/H). But the medians indicate, that *dec* is distinctly smaller than *alb*. With regard to these figures, some differences in size and form are identified between the species.

Table 1 Median, minimum, and maximum (in mm) of 22 characters, listed by species. Delimitation of characters mostly follows Janzon (1986), points of references were equidistant from the objective of the microscope. “Mag.” is the magnification used for measurements

Character	Mag.	Spec	Med.	Min.	Max.	Character	Mag.	Spec	Med.	Min.	Max.
head B (Janzon 1986)	80x	<i>alb</i>	0.903	0.763	1.094	pronotal collar (Janzon 1986)	160x	<i>alb</i>	0.097	0.063	0.134
	80x	<i>dec</i>	0.650	0.581	0.719		160x	<i>dec</i>	0.059	0.050	0.075
	80x	<i>sol</i>	0.856	0.794	0.888		160x	<i>sol</i>	0.088	0.075	0.100
head H (clypeus- lower edge)	80x	<i>alb</i>	0.675	0.600	0.800	marginal vein (Janzon 1986)	80x	<i>alb</i>	0.425	0.350	0.513
	80x	<i>dec</i>	0.500	0.438	0.569		80x	<i>dec</i>	0.325	0.281	0.363
median ocellus)	80x	<i>sol</i>	0.663	0.600	0.700		80x	<i>sol</i>	0.438	0.375	0.463
upper face (lower edge toruli-lower edge median ocellus)	80x	<i>alb</i>	0.388	0.344	0.463	postmarginal vein (Janzon 1986)	80x	<i>alb</i>	0.413	0.363	0.488
	80x	<i>dec</i>	0.294	0.256	0.331		80x	<i>dec</i>	0.319	0.275	0.344
	80x	<i>sol</i>	0.388	0.363	0.413		80x	<i>sol</i>	0.432	0.350	0.488
POL (Janzon 1986)	160x	<i>alb</i>	0.236	0.194	0.266	stigmal vein (Janzon 1986)	80x	<i>alb</i>	0.313	0.263	0.350
	160x	<i>dec</i>	0.181	0.156	0.191		80x	<i>dec</i>	0.231	0.206	0.250
	160x	<i>sol</i>	0.219	0.197	0.238		80x	<i>sol</i>	0.300	0.275	0.325
OOL (Janzon 1986)	160x	<i>alb</i>	0.133	0.119	0.169	metatibia (length of tibia)	80x	<i>alb</i>	0.813	0.694	1.013
	160x	<i>dec</i>	0.100	0.091	0.109		80x	<i>dec</i>	0.588	0.513	0.638
	160x	<i>sol</i>	0.150	0.141	0.163		80x	<i>sol</i>	0.763	0.688	0.819
eye H (Janzon 1986)	80x	<i>alb</i>	0.428	0.375	0.500	propodeum L (median area length, Janzon 1986)	160x	<i>alb</i>	0.166	0.125	0.213
	80x	<i>dec</i>	0.313	0.281	0.350		160x	<i>dec</i>	0.125	0.100	0.144
	80x	<i>sol</i>	0.400	0.369	0.425		160x	<i>sol</i>	0.181	0.159	0.200
eye B (Janzon 1986)	80x	<i>alb</i>	0.294	0.263	0.338	propodeum B (median area breadth, Janzon 1986)	80x	<i>alb</i>	0.394	0.319	0.513
	80x	<i>dec</i>	0.225	0.200	0.244		80x	<i>dec</i>	0.263	0.244	0.313
	80x	<i>sol</i>	0.263	0.250	0.275		80x	<i>sol</i>	0.375	0.338	0.425
pedicel L (length of pedicel in profile)	160x	<i>alb</i>	0.094	0.081	0.106	gaster L (Janzon 1986)	32x	<i>alb</i>	1.789	1.547	2.266
	160x	<i>dec</i>	0.075	0.069	0.081		32x	<i>dec</i>	1.266	1.094	1.406
	160x	<i>sol</i>	0.091	0.084	0.097		32x	<i>sol</i>	1.469	1.203	1.625
funicle L (length of first funicular segment in profile)	160x	<i>alb</i>	0.106	0.088	0.125	gaster B (Janzon 1986)	80x	<i>alb</i>	0.713	0.563	0.975
	160x	<i>dec</i>	0.066	0.050	0.075		80x	<i>dec</i>	0.500	0.413	0.563
	160x	<i>sol</i>	0.091	0.075	0.100		80x	<i>sol</i>	0.800	0.675	0.925
scape (Janzon 1986)	80x	<i>alb</i>	0.338	0.300	0.413	tergum 7 L (length of seventh gastral tergum, Janzon 1986)	80x	<i>alb</i>	0.288	0.231	0.388
	80x	<i>dec</i>	0.250	0.219	0.288		80x	<i>dec</i>	0.200	0.150	0.263
	80x	<i>sol</i>	0.313	0.281	0.338		80x	<i>sol</i>	0.225	0.172	0.238
malar space (Janzon 1986)	160x	<i>alb</i>	0.225	0.188	0.275	tergum 7 B (breadth of seventh gastral tergum, Janzon 1986)	80x	<i>alb</i>	0.278	0.231	0.325
	160x	<i>dec</i>	0.156	0.138	0.175		80x	<i>dec</i>	0.206	0.169	0.231
	160x	<i>sol</i>	0.200	0.175	0.222		80x	<i>sol</i>	0.300	0.213	0.344

Moreover, there may also be much redundancy in the data, as all characters are strongly intercorrelated (Spearman's ρ , $p < 0.01$ in all instances). Here, multivariate statistics offer convenient methods for a straightforward exploration of the data.

Table 2 lists the discriminant functions found in several different DAs of comparisons of species or groups of species. In a first analysis *sol* was compared with the other two species together but subsequently only single species were included for pairwise comparisons. In each of the four analyses a large number of variables were eliminated and only 9–11 characters were retained for the final model. The power of the discriminant function was always higher in the reduced than in the full model. Generally, the groups are widely separated for values of those discriminant functions (Fig. 2).

Table 2 Coefficients of different linear discriminant functions found with DA

	rest-sol	alb-sol	dec-sol	alb-dec		rest-sol	alb-sol	dec-sol	alb-dec
head B	–	–	3.959	–	malar space	–	–	–	7.597
head H	7.078	–	8.462	–	marginal vein	–	–	1.633	–
upper face	–5.806	–4.365	–9.148	–	postmarginal vein	1.700	2.317	–	–
POL	–3.259	–	–9.950	–	stigmatal vein	–	–2.474	–	–4.598
OOL	22.354	21.926	14.777	–	metatibia	–	–	–	3.873
eye H	–	3.859	–	–	propodeum B	–	–	–5.001	4.438
eye B	–	–7.366	–	–	gaster L	–0.946	–0.493	–	–1.334
pedicel L	–11.569	–11.530	22.605	–	gaster B	0.485	0.711	–	–
funicle1 L	–8.562	–	–13.512	–17.884	tergum7 L	–	–2.269	–1.996	4.212
scape	–5.466	–	–4.852	–11.115	tergum7 B	–	–	–	–6.094

With the DA the species can be very well separated using a subset of the characters only. However, it may be useful to know, whether the differences of the species are related to size or rather to form. To address this question, a PCA was computed using the ten characters retained in the first DA (rest-sol, Table 2). This PCA was very effective in further reducing the dimensionality of the data, as the first and second principal components comprise about 93% of the total variance. Hence, the remaining components can safely be neglected. The scatterplot of all 66 specimens against the values of the first two components (Fig. 3) shows that the species cluster tightly together. There is no overlap between the different species at all. The first component is strongly correlated with each of the original variables, that is its correlation coefficients ('loadings') are uniform (all positive) and very high (Table 3). It may therefore be considered as a 'size' vector (Manly 1994) rather than an 'allometry' vector (see Shea 1985). In other words, variation related to size is summarised in this axis. The second component, on the other hand, shows some high – positive or negative – correlation with only some of the original variables, e.g. OOL, gaster L, and gaster B (Table 3). Thus, variation related to shape differences is summarised in the second

component. With this rather rough but nevertheless important interpretation of the components in mind, it is evident that *sol* is clearly separated from *alb* by differences in shape and from *dec* by shape and size (Fig. 3). Contrary to this, *alb* differs from *dec* mainly in size.

Table 3 Correlation coefficients of principal components with original variables

Character	Component	
	1	2
head H	0.9937	-0.0186
upper face	0.9853	0.0418
POL	0.9379	-0.1683
OOL	0.8790	0.4150
pedicel L	0.9593	0.0075
funicle l L	0.9443	-0.2145
scape	0.9662	-0.1718
postmarginal vein	0.8990	0.1985
gaster L	0.8418	-0.4746
gaster B	0.8407	0.4196

Discussion

In the taxonomy of Pteromalidae, where qualitative characters for the separation of closely related species are frequently lacking, one has to rely on quantitative characters. Graham (1969), who was one of the first using morphometric measurements, calculated single ratios to discriminate among species. The above results demonstrate that such ratios are often insufficient for an unambiguous identification of species. This is also the case for *Pteromalus solidaginis* (*sol*), which is generally quite well distinguished from the other species. The best ratios (e.g. POL/OOL, gaster L/B) still show some amount of overlap with *P. albipennis* (*alb*). Eye H/B mentioned by Graham & Gijswijt (1991) as one of the key characters for the separation of *sol* from *dec* allows the classification of only 70% of the specimens (Fig. 1). This overlap is also likely to increase when more material also from other localities is available for study. Specimens of *sol* and *dec* originate from a few localities in Southern France and England respectively (Appendix) and their overall variation is thus distinctly smaller than in *alb* (Fig. 3). Therefore, the discriminant functions which were found in the DA, are much more valuable. They are based on the information of several characters and are thus more reliable and have a much better separating power (Fig. 2). A discriminant function is also a very useful tool for the identification of new specimens. In this respect, Flury & Riedwyl (1988) invented a practical method for which they coined the term identification analysis.

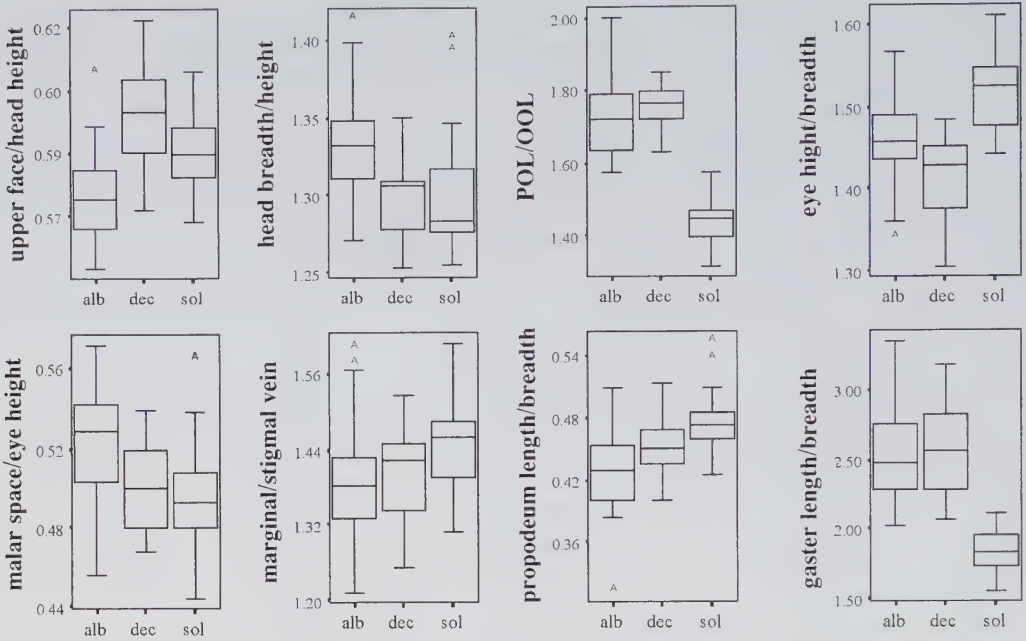


Figure 1 Box-and-whisker plots of eight ratios commonly used in Pteromalidae

According to the results of the PCA, *P. decipiens* (*dec*) is separated from *alb* mainly by its smaller size, despite the fact that their means may also be significantly different for values of the second principal component, the 'shape' vector (Fig. 3). The variance of this axis, however, is only 7.2% of the total variance, hence the differences related to shape may actually be negligible. Differences in size alone are not necessarily a good indication for separate species. For instance, it is well known from examples in parasitic Hymenoptera that specimens of the same species may vary significantly in size when reared from a different host species (Quicke 1997). Unfavourable conditions during development as caused by superparasitism are probably another source of such variation (resulting e. g. in 'dwarf' specimens). So, it might be questioned whether *dec* really deserves a specific status and is not just a form of *alb*. To address this problem, it is important to consider all available data. In this study it was found that some qualitative characters such as the sculpture of the propodeum, were also important. Further characters were mentioned by Graham (1969: 548) in the original description, for instance the colour and shape of the flagellum. These have actually been used by the author for identification of specimens prior to the morphometric analyses. Therefore, multivariate statistics simply represent an alternative in those cases where 'traditional' approaches fail to reveal the difference between taxa.

In conclusion, the application of DA and PCA reveals corroborated evidence of a separate species in the case of *sol*. It is distinguished from both *alb* and *dec* by clear differences in shape or shape and size respectively. On the other hand, it was not possible to further substantiate the status of *dec*, as it is separated from *alb* mainly by its smaller size. However, the results do not contradict earlier findings regarding qualitative morphology, hence the specific status of *dec* is retained.



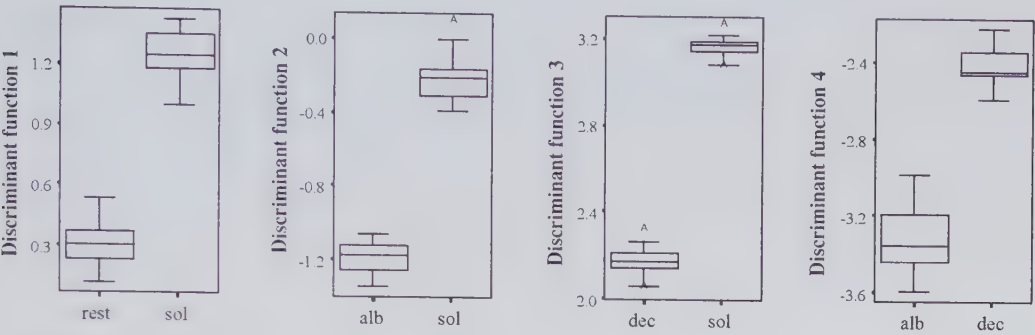


Figure 2 Box-and-whisker plots for values of the discriminant functions found in four different DAs (see Table 2). The separation of groups has strongly increased in comparison with the values of simple ratios (Fig. 1)

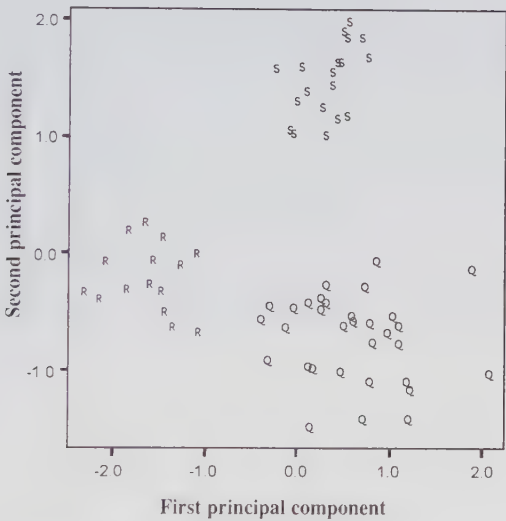


Figure 3 Plot of 66 specimens (+ alb, dec, sol) against values for the first and second principal component. The components comprise about 93% of the total variance

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Appendix

List of female specimens used for the data-matrix (number in square brackets). For abbreviations of depositories see acknowledgements.

Pteromalus albipennis (n=32): – ENGLAND: Cambs, Monks Wood (Straw), ex *Tephritis bardanae* (Schränk) (Diptera: Tephritidae), BMNH: 17.xi.1982 [1], 11.xi.1982 [1], Middlesex, Southgate (Graham), BMNH: 11.viii.1970 [1], 9.ix.1969 [1], 28.viii.1969 [1], 14.viii.1969 [2], 22.viii.1969 [3], 19.v.1970 [1]. – FRANCE: Bretagne, W Rennes, Guitté (Vidal), ex *Urophora quadrifasciata* (Meigen) or *Chaetorellia jacea* (Robineau-Desvoidy) (Diptera: Tephritidae), on *Centaurea nigra* L., VID: 8.ix.1995 [7]; Lozère, 2 km S Aleyrac (Baur), on *Senecio* sp., NMBE: 12.vii.1995 [3]; Lozère, Camprieux-Col de Faubel (Baur), NMBE: 13.vii.1995 [1]. – GERMANY: Niedersachsen, Göttingen, Rainshof (Denys), ex *Tephritis formosa* (Loew) (Diptera: Tephritidae), on *Sonchus oleraceus* L., VID: vii.1995 [6], 7.viii.1995 [2]. – SWITZERLAND: Wallis, Leuk, Brentjong (Baur), on *Achillea millefolium* L., NMBE: 15.vi.1996 [2].

P. decipiens (n=15): – ENGLAND: Berkshire, Newbury, Thatcham (Graham), paratype, BMNH: 29. viii.1964 [1]; Middlesex, Southgate (Graham), BMNH: 25.viii.1970 [4], 28. viii.1969 [5], 9.ix.1969 [1], 1.ix.1970 [4].

P. solidaginis (n=19): – FRANCE: Drôme, Séderon, Col de l'Homme Mort, on *Solidago virgaurea* L., paratypes, BMNH: (Graham) 15.viii.1988 [1], 1.viii.1990 [6], 27.viii.1990 [4], 15.viii.1988 [4], 1.viii.1990 [3]; (Gijswijt) 18.viii.1988 [1].

ON HYPOTHETIC ROUTES OF ECESIS OF *MICROTERTYS NIETNERI* (MOSTCHULSKY, 1859) (HYMENOPTERA: ENCYRTIDAE), AN EFFECTIVE PARASITOID OF COCCIDAE (HOMOPTERA)

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Abstract — The report contains general information on *Microterys nietneri* (Motschulsky) an important endoparasitoid of Coccidae, especially of *Coccus hesperidum* Linnaeus on citrus and other subtropical and tropical plants. The native area of *M. nietneri* is South East Asia, from where it penetrated by ecesis, i.e. with its hosts, into many regions of the world as well as into greenhouses. Some hypothethic ways of ecesis of *M. nietneri* are attempted to be reconstructed. The species has been purposely introduced only into Australia and New Zealand.

Key words: *Microterys nietneri*, Coccidae, ecesis, introduction

Introduction

Generalization of scattered information on important species of animals, plants and other organisms may be one of essential tasks of Systematics. It is especially true in the case of entomophagous insects which are still insufficiently studied. Only qualified taxonomists can estimate what a concrete species is, which are its relations to other species of the same genus, and check synonyms. Such work requires the study of type specimens, analysis of vast literature and personal field experience. The basic method for these studies and analysis is that of tritroph (in our case: parasitoid-phytophagous insect-host plant).

Our report is dedicated to the encyrtid *Microterys nietneri* (Motschulsky), a parasitoid of soft and some other Coccidae. Earlier it was known under the names *M. flavus* (Howard) and *M. frontatus* (Mercet) which are synonyms of *M. nietneri*. The senior author had the fortunate possibility to study types of all three species in museums of Russia (St. Petersburg, Moscow), Finland (Helsinki), Hungary (Budapest), England (London), France (Paris), Spain (Madrid), USA (Washington, Riverside, Berkeley) and Mexico (Cd. Victoria). We are thankful to curators of entomological collections of these museums for possibilities to study materials of *M. nietneri* and for their friendly help.

Geographic distribution of *Microterys nietneri* is very wide, but not cosmopolitan. We support the hypothesis of the South-East Asiatic origin of this species and try to speculate on possible ways of its penetration by ecesis, i.e. with its hosts (De Bach 1971; Trjapitzin & Sugonjaev 1987) into different regions of the world (for biological control purposes it was intentionally introduced only into Australia and New Zealand).

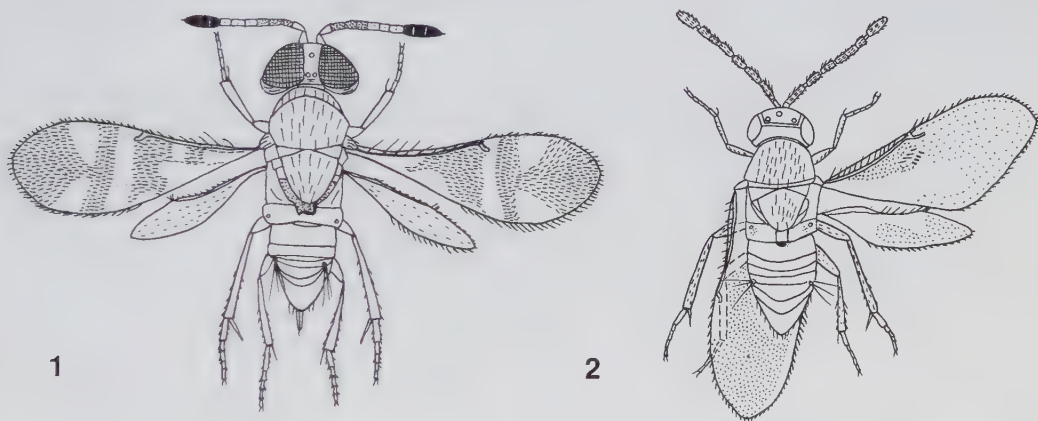
Microterys nietneri (Motschulsky, 1859)

(Figs 1, 2)

The species was described from Sri Lanka (Motschulsky 1859- as *Encyrtus*).

Synonyms: 1) *M. flavus* (Howard 1881) described from USA (California) (Howard 1881 as *Encyrtus*); 2) *M. frontatus* (Mercet 1921), described from Spain (Mercet 1921 as *Encyrtus*).

The most comprehensive descriptions of *Microterys nietneri* were published by Mercet (1921 as *Encyrtus frontatus*) and by Noyes (1988 as *M. flavus*). Immature stages of *M. nietneri* were investigated by Maple (1947 as *M. flavus*) and by Saakian Baranova (1968 as *M. flavus*); the a most important bibliography was collected by Peck (1963 as *M. flavus*) and Trjapitzin (1989).



Figures 1–2 *Microterys nietneri*: 1, female (ex Quayle 1911) (X 50); 2, male (ex Saakian-Baranova 1968)(x 50)

The species of *Microterys* more related to *M. nietneri* are *M. kotinskyi* (Fullaway 1913), described from Hawaiian Islands and *M. eleutherococi* Trjapitzin et Sugonjaev, 1972 described from the Far East of Russia. Beardsley (1976) synonymized *M. kotinskyi* with *M. nietneri* but we reject such a synonymy. *M. kotinskyi* differs from *M. nietneri* in the apical dark band of the forewing not connected with the central transverse dark band.

Microterys nietneri is an endoparasitoid of Coccidae. Its larvae belong to the encyrtoid type of development. In the instars 1–4, the larva is attached by two caudal spiracles to the aeroscopic plate of egg and breathes by atmospheric air, i.e., the larva is metapneustic. Larva of the 5 th instar is peripneustic, it has 9 pairs of open spiracles.

According to our recent knowledge, *Microterys nietneri* has the following geographic distribution (Fig. 3): Algeria (ecesis into the Mediterranean Sea Coast), Argentina (ecesis), Australia (introduced), Azerbaijan (ecesis into the subtropical zone of Lenkoran), Bangladesh, Belgium (in greenhouses), Bulgaria (ecesis), China (Sichuan and Guandong Provinces), Croatia (ecesis into the Adriatic Sea Coast), Cyprus (ecesis), Egypt (ecesis), Fiji (ecesis), France (Departments of Héralult, Var and Alpes-Maritimes)(ecesis), Georgia (ecesis into the subtropical

zone of Black Sea Coast), Germany (ecesis into a greenhouse and mass production in a commercial insectary), Greece (ecesis into Samos Island), Hawaiian Islands (ecesis), Honduras (ecesis), Hungary (ecesis into a greenhouse of Budapest), India, Iran (ecesis into the subtropical zone of the Caspian Sea Coast), Israel (ecesis and mass production in a commercial insectary), Italy (ecesis), Jamaica (ecesis), Lebanon (ecesis), Lybia (ecesis), Malaysia, Mexico (states of Tamaulipas and Morelos) (ecesis), Montenegro (ecesis into the Adriatic Sea Coast), the Netherlands (ecesis into a greenhouse and mass production in a commercial insectarium), New Zealand (introduced), Oman (ecesis), Republic of South Africa (ecesis), Russia (ecesis into the subtropical zone of Black Sea Coast of Krasnodar Territory and into greenhouses of Moscow), Spain, including Tenerife (ecesis), Sri Lanka, Turkey (ecesis into the subtropical zone of Black Sea Coast), the Ukraine (ecesis into Black Sea Coast of the Crimea), USA (ecesis into California, Texas and Florida and into greenhouses of Ohio and New Jersey; also mass production in commercial insectaries of California, Arizona and Michigan).

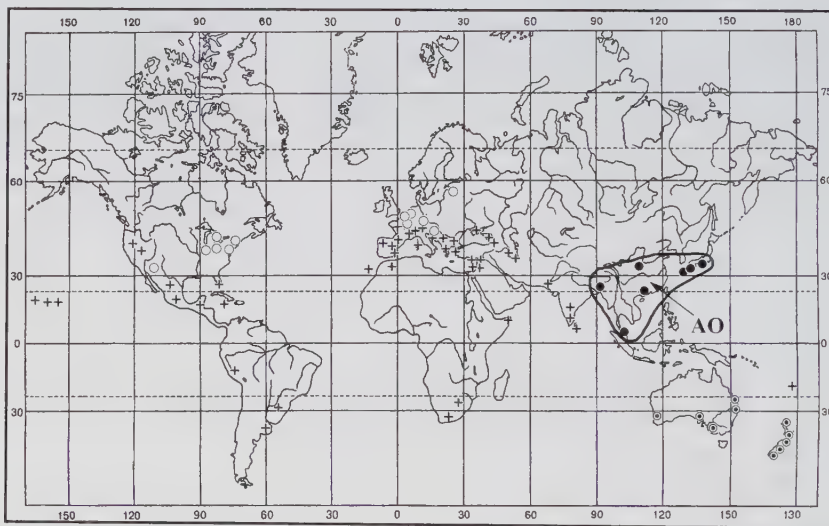


Figure 3 Geographic distribution of *Microterys nietneri* (original) (A.O. – – hypothetic area of the species origin, • foundings in the area of origin, + ecesis, § introduction, ° in greenhouses)

As one can see from these data, *Microterys nietneri* has been found in the true tropical regions of the world more rarely than in subtropical regions. It is probably absent or rare in the Tropical Africa, in Central America and in the Tropical South America. It might be supposed that its penetration with coccids (ecesis) into hot tropical regions is difficult, especially into dry tropics. This fact, possibly may be explained, at least partly, by the origin of *M. nietneri* in more or less humid subtropical and mountainous tropical regions of the South-East Asia where is also homeland of its principal host, the soft brown scale *Coccus hesperidum* Linnaeus, and of citrus, the preferable host plants of this coccid (Saakian-Baranova 1968; Trjapitzin 1968, 1981; Trjapitzin & Sugonjaev

1987; Izhevsky 1990). In the true tropics, *M. nietneri* has been found, according to our knowledge, only in Malaya, Bangladesh, India, Sri Lanka, Hawaii, Fiji, Jamaica, Mexico, Honduras and Peru, but we do not know conditions of its life there. Malaya, Bangladesh, India and, probably, Sri Lanka might be parts of the natural area of *M. nietneri*. In Sri Lanka the species has been collected in the central, mountainous part of the island where climate is less hot. In Hawaii and Fiji, the climate is stable, oceanic. In arid conditions, *M. nietneri* was found usually in more humid localities or habitats or in those places where irrigation is regular. Its area of distribution is less than the potential area for citrus cultures.

In its specialization of parasitism, *Microterys nietneri* is broadly oligophagous, because it attacks different species of the family Coccidae belonging to different genera. It is a polyvoltine species well adapted to its usual polyvoltine host, *Coccus hesperidum*, also due to their common homeland. In special conditions, *M. nietneri* can live also in tropics.

Hypothetic routes of ecesis of *Microterys nietneri*

Route 1. Western direction from the South-East Asiatic area of origin to the Mediterranean Region

This direction of ecesis of *Microterys nietneri* was postulated by Trjapitzin (1981) and Trjapitzin & Sugonjaev (1987). It was supposed that ecesis of *M. nietneri* and *Encyrtus aurantii* (Geoffroy), the common parasitoids of soft brown scale *Coccus hesperidum* on citrus and some other plants into the Caucasus and the Mediterranean Region, took place already in ancient times, in the period of conquests of Alexander the Great (Macedonian), and later through the Great Silk Way. But the connecting link of this route in Iran was unknown to us earlier. And only now this link was discovered both for *M. nietneri* and *E. aurantii* at Caspian Sea Coast of Iran. *M. nietneri* has been also found in Oman, in wet conditions.

In the subtropical zone of Black Sea Coast of Caucasus, *Microterys nietneri* is a common parasitoid of *Coccus hesperidum* from Batumi to Tuapse in the north. In Abkhazia, it penetrated into forests where it infests *C. hesperidum* on ivies (*Hedera* spp.).

Route 2. Western direction from the Mediterranean Region to America

There is no doubt that *Microterys nietneri* has been repeatedly introduced with coccids on different plants into America during Spanish, English, French and probably Dutch colonization of different American regions and islands.

Route 3. Eastern direction from Asia into America

This way of ecesis of *Microterys nietneri* during Spanish colonial times cannot be excluded, because trade relationships existed between Spanish colonies in America and China and Philippines.

By this route, the species could be accidentally introduced into Mexico and Peru, and later could penetrate from Mexico into California. But, it is probable also that *M. nietneri* penetrated into California in the second half of XIX century when great citrus industry was established there.

Route 4. Western direction from America to Hawaiian Islands

Most probably, *Microterys nietneri* penetrated accidentally into Hawaii at times of introduction of citrus and other plants by the North American colonization, but the route from Eastern Asia cannot be excluded.

Ways of ecesis of *Microterys nietneri* into South Africa are uncertain.

Programmed introductions of *Microterys nietneri*

For the purposes of biological control of coccids, *Microterys nietneri* has been successfully introduced into Australia (Wilson 1960; Malipatil *et al* 2000) and into New Zealand (Miller *et al.* 1936; Noyes 1988).

Microterys nietneri in greenhouses

In temperate zones of the Northern Hemisphere, *Microterys nietneri* has been found in greenhouses of USA, Russia and some other European countries. It is interesting to note that when this species was purposely introduced from USA into orangeries of the Principal Botanical Garden of Moscow, it was found that it was already present there (Ilyinskaya 1963). Liberations of *M. nietneri* in greenhouses of Moscow against *Coccus hesperidum* were very effective. Mass production of *Microterys nietneri* is carried out in some commercial insectaries of Germany, Belgium, the Netherlands, Israel and USA.

Application of *Microterys nietneri*

In Texas (USA), citrus orchards are concentrated in the extreme south of this state, near the Mexican frontier. Mass production of the parasitoid was well organized in a laboratory of Weslaco. The technique of mass production was described by Reed *et al.* (1968).

For the *Coccus hesperidum* outbreaks suppression of in citrus groves, schemes of pesticides application were changed in adjacent cotton fields and liberations of *Coccophagus lycimnia* Walker (Hymenoptera: Aphelinidae) and *M. nietneri* were undertaken in citrus plantations. There actions, together with the natural control effectuated by other parasitoids and predators, had as a result the restoration of complete biological control of *Coccus hesperidum* (Hart 1972; Browning 1990; Elzen & King 1999)

Conclusions

Microterys nietneri (Motschulsky) is an important parasitoid of Coccidae, especially of the soft brown scale *Coccus hesperidum* Linnaeus on citrus and on some other subtropical and tropical plants. It is rather well studied entomophagous insects: its bibliography number more than 160 literature sources. Its homeland is South-East Asia from where it has penetrated by ecesis, i.e. with the hosts on cultivated plants into many regions of the world. The example of *Microterys nietneri* strongly emphasizes the great role of ecesis in the natural control of noxious insects. This

contribution is a summary of our big manuscript dedicated to *Microterys nietneri* which is awaiting publication.

Many-sided studies of economically important entomophagous have great importance for estimation of the role of pests natural control and for development of classical biological control and integrated pest management in agrobiocenoses.

As concerns the hymenopterous family Encyrtidae, now there exists a serious need of a monograph on the most significant species, as well as in nature generally and in agriculture in the world scale. The work on preparation of such monograph in libraries and with insect collections would require several years with a condition of participation of taxonomists. We give here a tentative list of 31 encyrtid species which might be included in such a book: *Ageniaspis citricola* Logvinovskaya, *A. fuscicollis* (Dalman), *Anagyrus kamali* Moursi, *A. lopezi* (De Santis), *A. pseudococci* (Girault), *Anicetus annulatus* Timberlake, *A. beneficus* Ishii et Yasumatsu, *Avetianella longoi* Siscaro, *Blastothrix britannica* Imms, *B. longipennis* Howard, *Comperia merceti* (Compere), *Comperiella bifasciata* Howard, *Copidosoma floridanum* (Ashmead), *C. koehleri* Ev. Blanchard, *Diversinervus elegans* Silvestri, *Encyrtus aurantii* (Geoffroy), *E. infelix* (Embleton), *Holcorthorax testaceipes* (Ratzeburg), *Ixodiphagus hookeri* (Howard), *Leptomastidea abnormis* (Girault), *Leptomastix dactylopii* Howard, *Metaphycus helvolus* (Compere), *M. lounsburyi* (Howard), *Microterys clauseni* Compere, *Neodusmetia sangwani* (Subba Rao), *Ooencyrtus kuvanae* (Howard), *O. pinicolus* (Matsumura), *O. pityocampae* (Mercet), *Pseudaphycus malinus* Gahan, *Psyllaephagus pilosus* Noyes, and *P. yaseeni* Noyes. Reasons for selection of species in this list will require a special publication.

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SPECIES-LEVEL TAXONOMY OF MYMARIDAE (HYMENOPTERA): CURRENT STATUS AND IMPLICATIONS FOR BIOLOGICAL CONTROL OF LEAFHOPPERS OF ECONOMIC IMPORTANCE

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Abstract – Eleven genera of Mymaridae are identified as those for which reliable leafhopper (Cicadellidae) host records exist, and a brief overview is presented. Leafhoppers from the New World tribe Proconiini are indicated as known or potential hosts of many of the New World species belonging to the *ater* species group of *Gonatocerus* Nees.

Key words: Hymenoptera, Mymaridae, Cicadellidae, Proconiini, egg parasitoid

Introduction

Members of the family Mymaridae have been used in a number of programs against their leafhopper hosts, often as classical biological control agents (Huber 1986; Triapitsyn & Beardsley 2000). Many other leafhopper species, including potential pests of agricultural crops, are under effective natural biological control by mymarid egg parasitoids. These leafhopper-egg parasitoid complexes are usually poorly studied or unknown, even in Europe. Very few reliable host records exist for more than 1400 mymarid taxa; parasitoids of a much greater number of the leafhopper species are largely unknown. This creates problems for biological control workers, especially when certain leafhopper species spread beyond their natural range and become pests, or when natural biological control is disrupted by chemical treatments.

Identification of the egg parasitoid(s) is one of the first steps in any survey or program aimed at control of a certain leafhopper species. While economically important mymarids (including parasitoids of non-leafhopper hosts) may be relatively easy, with a few exceptions, to identify to genus using the available keys of Huber (1997) for the Nearctic region, Triapitsyn & Huber (2000) for the Palaearctic region, Yoshimoto (1990) for the New World, etc., at present their identification at the species level is difficult and often impossible. Except for a few countries, regions, or species groups, there are no identification keys available for the species in most speciose mymarid genera, such as *Anaphes* Haliday, *Camptoptera* Foerster, *Erythmelus* Enock, *Gonatocerus* Nees, *Polynema* Haliday and *Stethynium* Enock, which together comprise about 66% of all valid species recognized to date.

Host records are not known for many mymarid genera such as *Anagroidea* Girault, *Australomymar* Girault, *Neomymar* Crawford, *Onyomymar* Schauff, *Platyfrons* Yoshimoto, etc., the vast majority of species in which are undescribed. According to Huber (1986), representatives of 15 mymarid genera were known to have leafhoppers as hosts, but only 11 among those may be considered reasonably reliable: *Acmopolynema* Ogloblin, *Anagrus* Haliday, *Arescon* Walker,

Chaetomymar Ogloblin, *Gonatocerus*, *Himopolynema* Taguchi, *Mymar* Curtis, *Ooconus* Haliday, *Paranaphoidea* Girault, *Polynema*, and *Stethynium*. Members of *Erythmelus* are in fact parasitoids of Miridae, Tingidae and possibly of other Heteroptera (Triapitsyn, *unpubl. data*) although they perhaps may occasionally parasitize leafhopper eggs as well, but all such reports need confirmation along with similar records of leafhopper hosts for *Alaptus* Westwood, *Anaphes*, *Camptoptera*, and *Stephanodes* Enock. Therefore, for practical purposes, these last five genera are not considered in the below overview of the genera of Mymaridae that contain known parasitoids of Cicadellidae, with examples of the implications of the state of species-level taxonomy in those genera to biological control of some leafhopper species of economic importance.

Overview of the genera of Mymaridae associated with leafhopper hosts

Acmopolynema (almost cosmopolitan, except for western and central Palaearctic region): 46 valid species are currently recognized, a few either belonging to other genera or apparent synonyms of other species of *Acmopolynema*, and probably 80-100 species await to be described as new, mainly from the Neotropical region (Berezovskiy & Triapitsyn, unpublished data, a world revision is in preparation); identification keys to the described species are available for the Nearctic (Schauff 1981), Neotropical (Fidalgo 1989) and Palaearctic (Berezovskiy & Triapitsyn 2001) regions as well as for India (Hayat & Anis 1999a). Only one species, *A. sema* Schauff, was recorded from a leafhopper host, *Homalodisca insolita* (Walker) (Schauff 1981). I also reared many specimens of *A. sema* from eggs of this leafhopper on *Sorghum* sp. in southern Florida, USA, in August 2001; it is a candidate species for introduction into California as a classical biological control agent against closely related *Homalodisca* species.

Anagrus (cosmopolitan): 85 species are currently considered as valid, including 9 which are unrecognizable and a few that are apparent synonyms of other described species of *Anagrus*; probably 30-50 new species will need to be described (a world revision of the described species by E. Chiappini and S. V. Triapitsyn is near completion); many species have been reared from eggs of various leafhoppers in different habitats. Members of the genus are perhaps the most important parasitoids of small leafhoppers (including many economically important species) worldwide except for Australia and New Zealand, where *Stethynium* species are more prevalent (Triapitsyn, *in press*). Due to the minute size of *Anagrus* species, improper preserving or mounting techniques and the resulting misidentifications, as well as difficulties in associating parasitoids with the leafhopper species, many host records of *Anagrus* reported before 1989 are doubtful, though some of them have been corrected recently (Chiappini *et al.* 1996; Chiappini & Triapitsyn 1997; Triapitsyn 1997, 1998, 1999a, 1999b; Triapitsyn & Beardsley 2000). The above-mentioned references also contain identification keys to the described species for almost all zoogeographical regions except for the Afrotropical region. Taxonomy of *Anagrus* species parasitizing the rice-feeding leafhoppers and planthoppers (Delphacidae) in eastern Asia has been a problem that still needs attention; correct species identification will require studies that would combine morphological characters with data from cross-breeding experiments and molecular evidence. One such study (Chiappini *et al.* 1999) solved problems in recognition of four morphologically similar European species of *Anagrus*.

Arescon (almost cosmopolitan): about 20 valid species are currently recognized. Taxonomy of this genus is in flux, most of species are unrecognizable and no reliable identification keys are available other than for a few countries. Only one host record is from Cicadellidae (Huber 1986).

Chaetomymar (Old World except for western and central Palaearctic region): 7 valid species are currently recognized, several species were described in other genera, and a number of species are undescribed, mainly from the Afrotropical and Australasian regions; a key to the described species is in preparation (J. T. Huber, personal communication). The available records from leafhopper hosts (Huber 1986) are reliable.

Gonatocerus (cosmopolitan): This is by far the largest genus of Mymaridae; about 250 valid species are known; the number of undescribed species is difficult to estimate but it is almost certainly more than 300, mainly from the Neotropical, Afrotropical and Australasian regions; good identification keys are available for the species in certain countries such as Great Britain (Matthews 1986) and India (Zeya & Hayat 1995) as well as for the *ater* and *sulphuripes* species groups in the Nearctic region (Huber 1988). The numerous host records of *Gonatocerus* species from Cicadellidae are listed by Huber (1986, 1988). Species from the *litoralis* group appear to be the most difficult for identification; for instance, I failed to identify the two species which were imported (from Iran) and released in California against the beet leafhopper, *Circulifer tenellus* (Baker) (Walker *et al.* 1997).

In the New World, the amazing diversity of the *ater* group species, the majority of which (in the Neotropics north of Argentina) are still undescribed, could not be explained from the host-parasitoid point of view until recently, when the establishment of the glassy-winged sharpshooter, *Homalodisca coagulata* (Say), in California, USA, has prompted active search for its egg parasitoids. Surveys in California, Florida, Georgia, Louisiana, and Texas (USA) as well as in Nuevo León and Tamaulipas (Mexico) revealed complexes of mymarid egg parasitoids of several closely related *Homalodisca* spp. and *Oncometopia* spp., all of which (except for the above-mentioned *A. sema*) belong to the *ater* group of *Gonatocerus* (Triapitsyn *et al.* 1998; Triapitsyn & Phillips 2000). Considering the already known host associations of *ater* group species (Huber 1988) and the new host records that were established for such common North American species as *G. ashmeadi* Girault, *G. morrilli* (Howard), and *G. triguttatus* Girault (Triapitsyn *et al.*, *in press*), it has become evident that the majority of New World species from the *ater* group parasitize different genera in the leafhopper tribe Proconiini. The sharpshooters, which is the common name of the members of Proconiini, is exclusively a New World group which includes mostly large, xylem-sucking leafhoppers that are very diverse in the subtropics and tropics of the Neotropical region. Their eggs are also large in size and are laid in clusters. All the studied North American species of the *ater* group of *Gonatocerus* develop one adult wasp per host egg and thus the large size (body length more than 2 mm) of some undescribed tropical species of *Gonatocerus* from Central and South America, many of which belong to the *morrilli* subgroup of the *ater* species group as defined by Huber (1988), may be by mere correlation in size associated with several proconiine genera that reach 20 mm or more in length (Young 1968). Unfortunately, no positive host records exist to support such a conclusion yet, but there is no doubt in my mind that they will be obtained eventually.

Himopolynema (Australasian, Oriental, and eastern Palearctic): 6 valid species are currently recognized, a number of species are still undescribed, mainly from the Oriental region; identification keys to the described species are available (Hayat & Anis 1999b; Taguchi 1977). The record of *H. hishimonus* Taguchi from the leafhopper host, *Hishimonus sellatus* (Uhler) (Taguchi 1977), is complimented here by a new one as follows: 3 females, Japan, Fukuoka, IX.1967, K. Yasumatsu, ex. overwintering eggs of *H. sellatus* on mulberry [material in the collections of University of California at Berkeley and Riverside, USA]. It appears that this genus is associated with various Auchenorrhyncha on trees. For instance, an unidentified species of *Himopolynema* is a parasitoid of *Hindola* spp. (Machaerotidae) on clove trees in Indonesia (Balfas *et al.* 1990, who misidentified it as *Acmopolynema* sp.; S.V. Triapitsyn, *unpubl. data*).

Mymar (cosmopolitan except for South America south of Colombia and Venezuela): 8 valid species are currently recognized and about as many are undescribed (S.V. Triapitsyn & V.V. Berezovskiy, unpublished data, a world revision is underway); a key to the described species is available for the world (Triapitsyn & Berezovskiy 2001). The only record from a leafhopper host is that of *M. taprobanicum* (Ward) from *Nephotettix cincticeps* (Uhler) (Huber 1986). The genus apparently is associated with leafhoppers and planthoppers (Delphacidae) on grassy vegetation and is best collected using yellow pan traps.

Ooetonus (nearly cosmopolitan, except for South America, but restricted to temperate climates and high altitudes in the subtropics and tropics): 59 valid names and a number of undescribed species for which no identification keys are available except for the outdated keys to the British and the described North American species. Huber (1986) listed the published host records of *Ooetonus* including two from Cicadellidae.

Paranaphoidea (Australasian): 10 described species, all from Australia (no identification key is available), where this genus is quite common. *Eurymela distincta* Signoret is reported here as the first known host of an unidentified *Paranaphoidea* sp. (one specimen in the Australian National Insect Collection, Canberra, Australia).

Polynema (cosmopolitan): about 270 valid names. Taxonomically, this is arguably the most difficult genus in the Mymaridae. *Polynema* is at this point an unmanageable conglomerate of closely associated genera and subgenera, species identification of which is practically impossible. Many of the Australian species described by A. A. Girault are in fact members of other genera, both described and undescribed. The numerous European species of *Polynema* described by Soyka (1956, etc.) badly need a careful revision and largely must be synonymized either under each other or with species described earlier by other authors (a similar situation occurs with Soyka's species of *Anaphes*). Host associations of some species of *Polynema* (in the broad sense) were indicated by Huber (1986); a number of them parasitize eggs of economically important leafhoppers (small to medium-size). The two following examples illustrate the negative implication of the poor state of taxonomy of this genus to biological control: in one case, it prevented me from identifying the two species of *Polynema* which were imported (from Iran) and released in California against *C. tenellus* (Walker *et al.* 1997) and in the other, I have been unable to put a name to a *Polynema* sp., an egg parasitoid of the blue-green sharpshooter, *Graphocephala atropunctata* (Signoret), a vector of the Pierce's disease in grapes in North America (S.V. Triapitsyn, *unpubl. data*).

Stethynium (nearly cosmopolitan, except for South America): 54 valid species, most of which were described by A.A. Girault from Australia. Non-Australian species were revised by Huber (1987); no identification keys are available for the Australasian species where (especially in Australia and New Zealand) *Stethynium* is very common and diverse, apparently replacing *Anagrus* as the most important mymarid genus parasitic in eggs of the small leafhoppers (Triapitsyn in press). A revision of the Australasian species of *Stethynium* is thus much needed; unfortunately, many type specimens of Girault's species of *Stethynium* are in very poor condition and therefore such a revision must be based primarily on a careful preparation and examination of freshly collected material. The Holarctic species *S. triclavatum* Enock is a known parasitoid of *Empoasca vitis* (Goethe) on grape in Europe; its other host associations are indicated by Huber (1987).

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EUROPEAN *PODAGRION* (HYMENOPTERA: TORYMIDAE): EVIDENCE FOR THE PRESENCE OF SIBLING SPECIES

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Abstract. — A morphometric study on European *Podagrion* provided evidence for the existence of several different species. Specimens were collected from the fields and also from isogenetic strains representative of putative species, including one undescribed. We also performed crossing tests between 3 species to assess a possible reproductive isolation between putative species. A partial ecological barrier was found as well as, at least for one species, an absolute barrier concerning the mating behaviour.

Key words: *Podagrion*, Torymidae, Europe, morphometry, reproductive isolation

Introduction

Podagrion species are well known parasitoids of egg-mantids cases. Available keys for the west palearctic species (Nikol'skaya 1952; Zerova & Seryogina 1999) deal only with two species. However the examination of samples from Europe and the Mediterranean basin revealed that at least 6 species are actually present, and through the examination of the available types we could name *Podagrion pachymerum* (Walker), *Podagrion splendens*, Spinola a neotype of which is currently being designated, *Podagrion pachymerum gibbum* Bernard, initially described as a variety, *Podagrion klugianum* (Westwood) – quoted in the literature as *P. meridionale* Masi, a junior synonym of *P. klugianum*, **syn. nov.**, and *Podagrion minus* Strand. The general aim of our study is to revise the euro-mediterranean *Podagrion* and provide morphological characters to separate the species. Unfortunately most of the species are very close, if not sibling, and mostly quantitative characters are available to separate them. Moreover we do not know the range of intraspecific and allometric variation, especially in relationships with the environment, particularly the hosts.

Therefore the aims of this study are: 1) Screen the influence of the mantid host on the morphological characters of the parasitoids 2) Select characters for the separation of *Podagrion* spp. 3) One apparently undescribed species being widely distributed, compare the European and Afrotropical specimens; 4) Test the possibilities of the putative species found in South of France to interbreed; 5) Establish the status of *Podagrion pachymerum gibbum*, initially described as a variety.

Materials and Methods

Morphometric study. Only females were considered as males are of several morphological types and less numerous. Measurements and ratios used in this study are listed in Table 1. They were taken directly on the stereomicroscope. The angles between the propodeal carinae were calculated after drawing the propodeum with a camera lucida.

Effect of the mantid host on the *Podagrion* morphology. All series of the different *Podagrion* species were initially reared from one female; they were therefore each one isogenetic. The females offspring were mated with their brothers. The species studied were *Podagrion pachymerum*, *Podagrion splendens*, *Podagrion* sp. The cultures were made at 22–25°C on freshly deposited egg-cases of different mantid hosts. Table 2 details the hosts used for the cultures. A two-way analysis of variance was performed using the SAS package with respectively the strain and the host as sources of variation.

Screening of the quantitative characters and clustering analysis. The specimens came from samples reared during the survey of the parasitoids of mantid egg-cases; they were mostly collected in Languedoc (South of France) but some samples came from Greece, Morocco and Burkina Faso. Table 3 indicates for each mantid host and *Podagrion* sp. the number of specimens and their origin when not collected in the South of France. A clustering analysis was performed with the Winstat package, from euclidian distance, the agregation criterion being the momentum of order 2. We used the following variables: ratios ocelli, flagellum, propodeum, SETAE and BEND (Table 1), selected from the above study.

Table 1 Measurements and ratios used in the morphometric study (F1, 1st funicular segment; F7, 7th funicular segment; L, length; OCD, posterior ocelli diameter; OOL, ocell-ocular length; W, width)

Ratio	Measurements
ratio head	head W:head L
ratio ocelli	OOL:OCD
ratio flagellum	Pedicel + Flagellum:head W
ratio F1:Pedicel	F1 L:Pedicel L
ratio F1	F1 L:F1 W
ratio F7	F7 L:F7 W
ratio clava/head	clava L:head W
ratio head/thorax	head W:thorax L
ratio propodeum	propodeum L:propodeum W
AMP	angle between propodeal carinae at the base of the propodeum
ABP	angle between propodeal carinae at the mid length of the propodeum
BEND	(AMP–ABP):AMP
CUB	number of setae on the cubital fold of the fore wing
BAS	number of setae on the basal fold of the fore wing
SETAE	CUB – BAS

Reproductive isolation. The couples included virgin females and newly emerged individuals, less than 10 days old. The following couples were screened:

Γ <i>Podagrion</i> sp.	X	E <i>Podagrion pachymerum</i>
Γ <i>Podagrion pachymerum</i>	X	E <i>Podagrion</i> sp.
Γ <i>Podagrion</i> sp.	X	E <i>Podagrion splendens</i>
Γ <i>Podagrion splendens</i>	X	E <i>Podagrion</i> sp.
Γ <i>Podagrion gibbum</i>	X	E <i>Podagrion pachymerum</i> (trials in reduce number)

Table 2 Specimens used to study the effect of the mantid hosts on the morphology of Podagrion

Podagrion Species Hosts (in culture)	<i>Podagrion</i> sp.	<i>Podagrion</i> <i>pachymerum</i>	<i>Podagrion</i> <i>splendens</i>
<i>Ameles decolor</i>	0	0	17
<i>Ameles maroccana</i>	22	25	0
<i>Blepharopsis mendica</i>	25	25	0
<i>Empusa pennata</i>	12	17	25
<i>Mantis religiosa</i>	0	25	6

Table 3 Specimens used to screen the morphometric data in European Podagrion

Species Hosts	<i>Podagrion</i> <i>gibbum</i>	<i>Podagrion</i> sp.	<i>Podagrion</i> <i>pachymerum</i>	<i>Podagrion</i> <i>splendens</i>
<i>Ameles decolor</i>	7	0	0	0
<i>Ameles spаланzania</i>	1	0	0	0
<i>Empusa pennata</i>	5	16	0	0
<i>Iris oratoria</i>	30	0	0	0
<i>Mantis religiosa</i>	0	8	300	28
<i>Sphodromantis viridis</i> Morocco	0	7	0	0
<i>Sphodromantis lineola</i> Burkina Faso	0	25	0	0
Total specimens	43	56	30	28

The observations were made in Petri dishes of 50 mm and 10 mm height; all events were scored and timed; time observation was 15 mm per trial; some trials were made on egg-cases, when females emerged. The controls concerned male activity through intraspecies crossings, the sperm transfer through dissections of spermathecae and the sex ratio of the progeny.

Results and Discussion

Morphometric study

Effect on the mantid host on the *Podagrion* morphology

12 from the16 selected variables were very sensitive to the species as source of variation with F values ranging from 824.71 for the ratio SETAE to 12.42 for the ratio flagellum; they were all significant at 0.0001 probability. All but one variables were also sensitive to the host but with F values much lower; F ranges, for the 5 less sensitive variables, from 4.15 to 0.70, with the variable BEND not sensitive at the probability of 0.0001.

Screening of the quantitative characters and clustering analysis

The results of the analysis are represented on Fig. 1. The figure shows that the pattern of branching of the dendrogram almost exactly follows our initial segregation of specimens ($n = 156$) into putative species. Only 4 specimens of *Podagrion* sp. are mixed with those of *P. gibbum*; they come from Morocco and were reared from *Sphodromantis viridis*. On the terminal branching, intraspecies specimens reared from different hosts are generally mixed together, as well as specimens collected from different localities. Nevertheless 20 specimens of *Podagrion* sp. from West Africa come together but 5 others are mixed with specimens from Europa.

Reproductive isolation

As mating mostly takes place on the mantid egg-cases when females emerge, specificity to (a) certain host(s) may be important in species isolation. *Mantis religiosa* is the usual host for *Podagrion pachymerum*, *Podagrion splendens* and *Podagrion* sp. in South of France (see also Table 3). Latter species is most frequently reared from *Empusa pennata* but *P. splendens* is

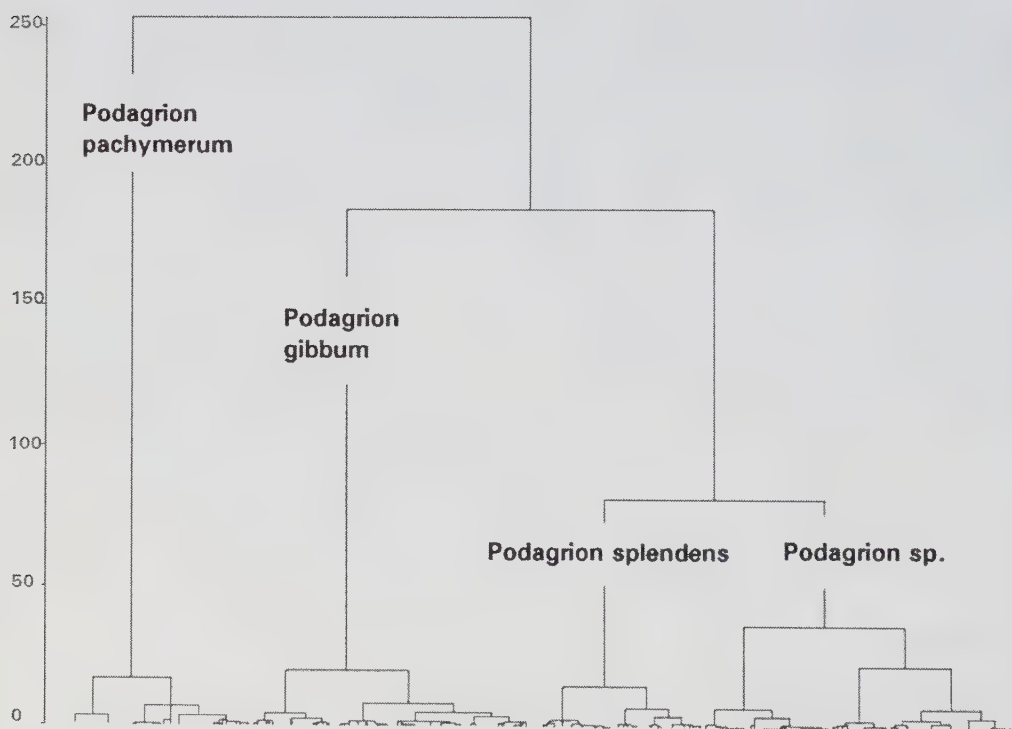


Figure 1 Dendrogram achieved from the clustering analysis showing the pattern of distribution of 156 specimens belonging to 4 putative species of *Podagrion*, using 5 variables. The 4 main branches agree with the initiation segregation of the specimens within the species except 4 individuals of *Podagrion* sp., which are mixed with those of *P. gibbum*

sometimes reared from the same host and *Podagrion gibbum* rarely so. Latter species is frequently associated with *Iris oratoria* and *Ameles decolor*, mantids spp., which never serve as hosts for the other *Podagrion* spp. Therefore a partial ecological isolation for *P. gibbum* certainly exists.

All active males of *Podagrion* reacted to the presence of females whatever the species was. Most of the active males of *P. pachymerum*, *P. splendens* and *Podagrion* sp. succeeded when trying to mount virgin females of other *Podagrion* spp.

The sexual behaviour in *Podagrion* is basically the same in all species studied (see also Grissell & Goodpasture 1981). On the egg-cases can we observe a pre-emergence behaviour, the purpose of which is to stimulate the activity of the female in order to emerge. This first sequence is followed by an emergence behaviour where the male pulls off the female from the egg-case and mounts her. The key sequence is the mounting that would introduce receptivity of the female for copulation. The patterns mainly includes 2 sequences: 1) Flagellum vibrations of male antennae, on each side

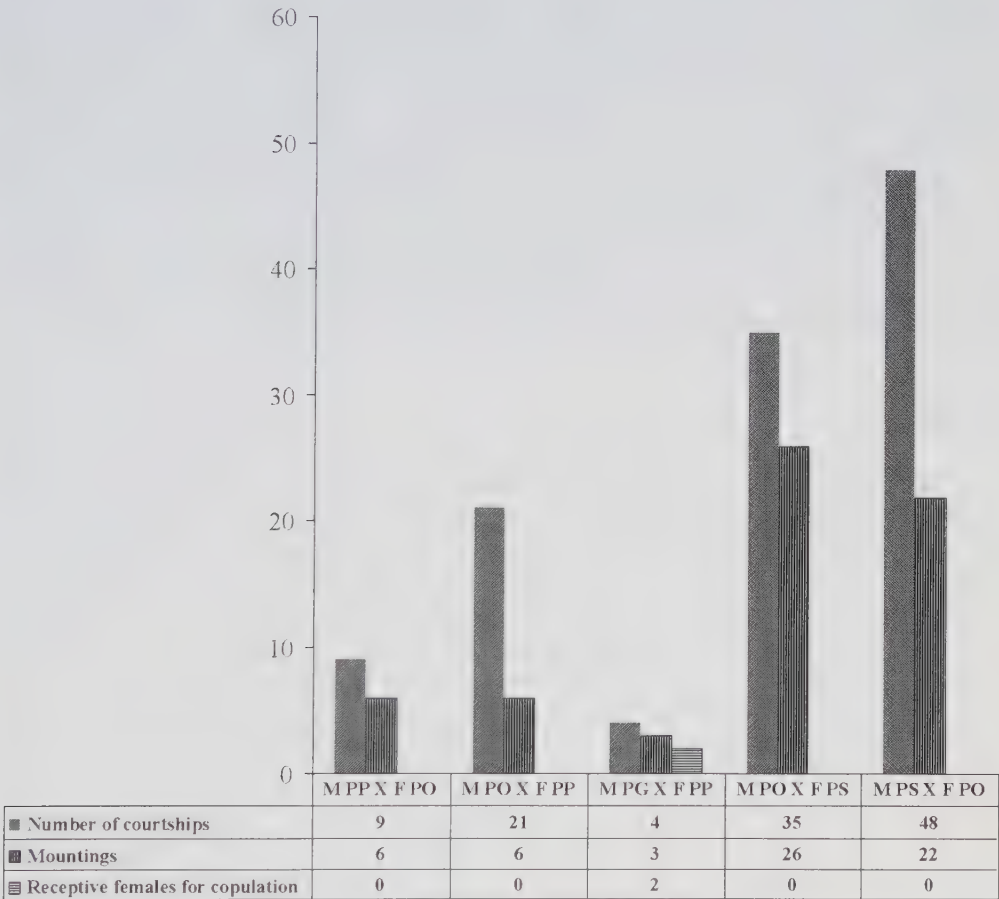


Figure 2 Study of reproductive isolation in European *Podagrion*: success of mating in interspecies crossings

of the female antennae (still with their exuviae) 2) Irregular wing flapping of the male, immediately followed by regular and quick flapping; this is the key signal which activates the female receptivity for copulation; the female does apparently not give out any signal in return to the male but exposes her genital opening. This sequence is immediately followed by copulation. In *P. pachymerum*, *P. splendens* and *P. gibbum*, the male flapping is continuous and regular. Conversely in *Podagrion* sp. can we observe a series of 5–12 short flappings with quick breaks between them. Elsewhere from the mantid egg-case, the previous pre-emergence behaviour of the male is replaced by a courtship behaviour.

Most of the intraspecies crossings were successful. According to the species, between 80% (in *Podagrion* sp.) to 100% (in *P. gibbum* but there with only 4 repetitions) of the males succeeded to copulate with females. Dissections showed that sperm transfer was effective in 100% of the cases and 100% of the progenies included at least one female.

The results in interspecies crossings can be seen in Fig. 2. The number of occurrences is sometimes reduced, especially in the crossings involving individuals of *P. pachymerum*, because few males of that species were active during the time of the experiment. In spite of this, a number of males did mount the females, exhibiting the mounting behaviour and gave out a precopulatory signal (wings flapping). But all trials involving individuals of *Podagrion* sp. were negative. The experiment is of course more conclusive in the interspecies crossing *P. splendens* X *Podagrion* sp., where more repetitions could be achieved. An interesting result concerns the crossing *P. gibbum* X *P. pachymerum* (but the trials are in reduced number). From the 4 crossings, 2 copulations were observed. The relevant females were dissected and sperm transfer appeared effective. The progeny of one of these females could be observed and included only males. In this case there is apparently no reproductive isolation through the mating behaviour but a postzygotic barrier might apparently be involved. Nevertheless much more repetitions are needed to conclude.

Conclusion

Four species of *Podagrion* at least are present in South of France. According to its morphological characters and the apparently reproductive isolation from *P. pachymerum*, *P. gibbum* should be upgraded to a valid species. *Podagrion* sp., still an undescribed species, is common and widely distributed; it is being described in a revisionnal work. A clear barrier exists in the sexual behaviour, between *Podagrion* sp. on one side, *P. pachymerum* and *P. splendens* on the other side. A partial ecological barrier, through the nature of the host, exists between *P. gibbum* and other the *Podagrion* spp. Males of *P. gibbum* can apparently mate females of *P. pachymerum*, but an apparent postzygotic barrier might be present; further evidence is needed to confirm this point. The signal launching female receptivity for copulation is a wing flapping, apparently specific to each species.

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TROPHIC LINKS AND PROBABLE DIRECTIONS OF PTEROMALID BIOLOGICAL EVOLUTION (HYMENOPTERA: CHALCIDOIDEA: PTEROMALIDAE)

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Abstract – On the Palaearctic material the main trends of the biological evolution of parasitic wasps of family Pteromalidae are discussed. The idiobiontic direction is assumed to represent itself the main trend in the evolution of parasitism among pteromalids.

Key words: biological evolution, idiobiontic ectoparasitism, koinobiontic endoparasitism, secondary parasitism, primary and secondary parasites

Introduction

The family Pteromalidae is one of the most vast families of Chalcidoid wasps (more than 4000 species in the world fauna and about 1500 species in the Palaearctic fauna). They have a universal distribution, but in moderate latitudes they are met with much more frequently than in the tropics. The pteromalids are an important group of entomophagous insects as they perform a natural control of many arthropods, for the most part insects. At the same time the potential possibilities of the practical utilization of pteromalids remain unrealized because their biology and their role in nature have not been sufficiently investigated. That is why the directions of the biological evolution of pteromalids may be discussed only in a more general way.

The analysis of trophic links of pteromalids was made formerly by the author (Dzhanokmen 1988, 1990, 1993). The data obtained in the course of this study permitted not only to confirm with new facts the previously observed character of trophic links of pteromalids, but to reveal new features in these links as well, and also to understand the biological diversity and the main trends of the biological evolution of the family. In the limits of the present report the account and comprehension of the material has been realized within the range Palaearctic fauna. The high taxonomic diversity of pteromalids in this region testifies about the rightfulness and advisability of the analysis accomplished here.

It should be admitted that all the particularities of trophic links between pteromalids and hosts are far from being exhausted by the enumeration of examples known to the science, nevertheless they obviously demonstrate that the diversity of hosts and of ways in which they are utilized by pteromalids is very ample. Numerous examples convince us that the overwhelming majority of species parasitize on insects with complete metamorphosis (Holometabola): Coleoptera, Hymenoptera, Diptera, Neuroptera, Strepsiptera and Siphonaptera. Some species develop on insects with uncomplete metamorphosis (Hemimetabola): Homoptera, Hemiptera, Blattodea. However, among them in the Palaearctic region only representatives of the first two orders were observed as hosts, the most part of them being secondary hosts. A few pteromalids are also linked to the egg cocoons of spiders (Arachnida, Araneina) from families Araneidae, Dytinidae,

Thomisidae and Uloboridae. In case of links with spiders these Chalcidoid wasps behave both as predators and as parasites. In egg cocoons of spiders pteromalids may predate on their eggs like those species which predate on coccid eggs, or parasitize on predators of eggs and, in particular, on Ichneumonid wasps larvae or in fly puparia.

The main feature in the biology of Chalcidoid wasps of family Pteromalidae consists in the predominance of ectoparasites in comparison with endoparasites. Pteromalids develop chiefly on larvae and pupae and very rarely on eggs and imago. Pteromalids may be both solitary and gregarious parasites as well as primary and secondary. Being secondary parasites they are, as a rule, asynchronic, and infest mature larvae of primary parasites, which have already finished to feed on the primary host.

Taking into account the predisposition of pteromalids to secondary parasitism, ectoparasitic pteromalids should be regarded with the outmost care as they represent entomophagous insects, which are used with the purpose of introduction for the biological suppression of arthropods damaging agri –and silviculture.

Discussion

Proceeding to the discussion of the possible trends of biological evolution of pteromalids we must first of all indicate the particularities of the fauna of these chalcidoid wasps of the Palaearctic region. They are as follows: the predominance of the subfamily Pteromalinae over the others taken together; the high level of generic differentiation; an extremely high level of secondary parasitism; the presence in the family of numerous taxa (including genera, tribes and subfamilies), wholly or to a considerable degree specialized on Coleoptera: Pteromalinae (many genera and the tribe Trigonoderini), Macromesinae, Chrysolampinae, Cleonyminae, Colotrechninae, Cerocephalinae).

The general analysis of the biological evolution of Chalcidoidea has been very convincingly realized by Kasparyan (1996). My task is the discovering of the key events in the evolution of pteromalids and the evaluation of their consequences.

In discussing the directions of pteromalid biological evolution the author proceeds from the nowadays widely spread point of view that the ectoparasitism on cryptic hosts dwelling under the bark of trees –most likely Coleoptera and /or Hymenoptera (Victorov 1959; Tobias 1967; Belokobylskij 1996) – is original for all types of parasitic wasps parasitism.

It seems to be more probable that the ectoparasitism on hidden Coleoptera larvae (bark beetles and other xylophagous beetles) is original or close to original state for family Pteromalidae (Table). Such a biological peculiarity is also characteristic of many recent species of the family.

It would be of interest to note that the morphological analysis of pteromalids imago showed that representatives of the on the whole less specialized subfamily Pteromalinae and the more specialized Macromesinae, Cerocephalinae and Cleonyminae subfamilies may be found precisely among species developing at the expense of larvae of such beetles. On the one hand this points to the probably ancient connections of pteromalids with this ecological and taxonomic host group, on the other hand it shows that these connections could have been preserved despite the high level of general morphobiological specialization (as in the case of all Chalcidoidea in comparison with Ichneumonoidea). The transition of these ectoparasites from one host to other cryptically dwelling hosts, namely to Diptera, Hymenoptera and Lepidoptera larvae supposedly occurs quite easily. This

is evidenced by the frequency of larvae parasites of bark beetles and other cryptically dwelling xylophagous beetles larvae in one and the same genera. On the basis of pteromalid trophic links analysis the major transformations of parasitism types in this family have been disclosed.

The next stage in the pteromalid biological evolution was ectoparasitism on larvae in cocoons and primarily in Hymenoptera cocoons (Tenthredinoidea, Sphecidae). First they probably infested those cocoons that were located in the wood and stems of grasses (some species of the *Mesopolobus*, *Habritys* and *Norbanus* genera) and later the cocoons hidden in the surface-soil and in the plant litter (species of the *Tritneptis* genus). The latter are specialized parasites in Tenthredinidae cocoons, which testifies to their ancient connection with this group of hosts and to the ancient character of this type of parasitism (idiobiontic ectoparasitism).

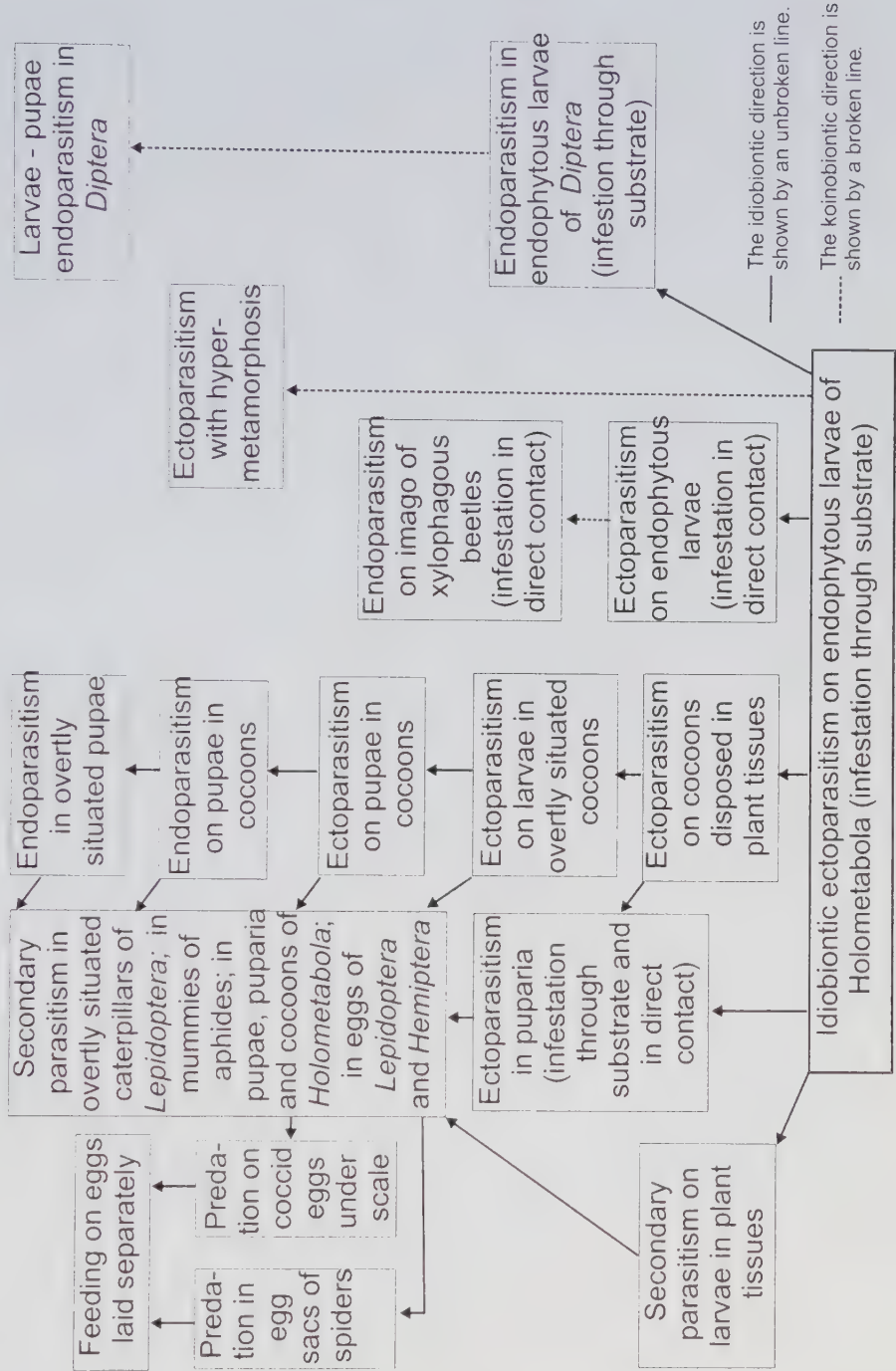
From larvae infestation in cocoons most likely there occurred a transition to pupae infestation in cocoons and in Diptera puparia. Apparently the settlement on both went on parallelly. This can be seen at least from the fact that *Habritys brevicornis* (Ratzeburg) are usually parasites of Sphecidae cocoons in rotten wood (Askew 1962; Dzhankmen & Kazenas 1974), but some cases of this species rearing from the puparia of xylophagous flies *Pachygaster meromelas* (Dufour) (Stratiomyidae) that were collected under the bark of horse chesnuts (Askew 1962). It would be appropriate to remark that the taxonomic composition of pteromalids hosts is frequently predetermined not so much by their taxonomic affinity as by the resemblance in the appearance of the infested items.

Features of a higher specialized idiobiontic ectoparasitism are observed in pteromalids: among them females infest the cryptic host larva, paralyzing it by direct contact. For example, the female of *Xiphydriophagus meyerinckii* (Ratz.) (Pteromalinae), entering the old tunnel of the host *Xiphydria camelus* (L.) (Symphyta: Xiphydriidae) gnaws through the wood a tunnel leading to the gallery with its larva. Having penetrated into the gallery, the pteromalid female paralyzes the host larva and lays her eggs on it. The adult offspring of the parasitic wasp leaves the gallery using the maternal route (Graham 1969). The obvious complication in the pteromalid female behaviour lies in the fact that it gets into direct contact with the host (and not through the wall of the substrate which includes the object that is being infested).

One of the most important phenomena of pteromalid biological evolution is their transition to secondary parasitism. Practically all secondary parasites are ectoparasites. In most cases parasitic Hymenoptera become their primary hosts. They in their turn also dwell in a cryptic way (in cocoons, under the covering of a secondary host, in various types of cavities occupied by a secondary host). Thus it is quite evident that they have entered the host range of ectoparasitic pteromalids through the shifting of these last from their hosts to the primary parasites of these hosts. The fact that the primary host of pteromalids develops in/on the body of the secondary host has also apparently contributed to the utilization of primary parasites by pteromalids. The secondary host of pteromalids could originally have been the primary one. Thus it is not by chance that both primary and secondary parasites linked to one and the same host can be present in the same genus. But what is more important is that one and the same species can manifest itself both as a primary and as a secondary parasite. This can be most frequently observed in *Pteromalus*, *Mesopolobus*, *Dibrachys*, *Spaniopus*, *Homoporus*, *Callitula*, *Psychophagus* and other genera.

The evolutionary perspectiveness of secondary parasitism is more than evident. Being unable to compete with other parasitic Hymenoptera and Diptera in utilizing Holometabola and Hemimetabola the pteromalids have adapted themselves to developing on their primary parasites.

Figure 1 The relation of idiobiontic and koinobiontic trends in the biological evolution of family Pteromalidae



The secondary host started to be used as a shelter under whose cover the pteromalid immature stages develop.

This direction of pteromalid biological evolution has apparently appeared during ectoparasitism formation on cryptic Holometabola larvae. The consequences of this evolutionary event have manifested themselves in a particularly strong way later – in the process of utilization of overt developing stages of Holometabola (Lepidoptera, Hymenoptera, Diptera and Neuroptera) and Hemimetabola (Homoptera and Hemiptera). It is clear that the hosts cryptic way of life gave certain privileges to pteromalids since it provided them with a peculiar microclimatic conditions autonomous from the external environment. This helped them to go through the immature stages and safeguarded them from predators. At the same time cryptic mode of life imposed certain constraints limiting the family biological progress since many overtly developing taxonomic and ecological groups of Holometabola and almost all Hemimetabola have found themselves outside the adaptive zones occupied by the pteromalids. The evident advantages of secondary parasitism have contributed to a taxonomic diversity of pteromalids. A combination of a weakly specialized parasitism type (idiobiontic ectoparasitism) with a wide spectrum of new hosts has caused a powerful radiation within the new adaptive zones. To confirm what has been stated it would be sufficient to remind that most of the secondary parasites are found among the largest pteromalid genera and most of these species are morphologically slightly distinguishable.

It is easy to imagine and even to follow *in statu nascendi* the transition from secondary parasitism in cocoons and under the cover of a secondary host to predatory activity in spiders egg cocoons which is the case in genera *Dibrachys*, *Pteromalus*, *Trichomalopsis* (Pteromalinae) as well as to predation on insects eggs which can be seen in the *Eunotus*, *Moranila*, *Scutellista*, *Ophelosia* (Eunotinae) genera whose larvae consume the eggs under coccid scale. It should be taken into account that *Moranila californica* and *Ophelosia crawfordi* either are predators of coccid eggs or are ectoparasites on larvae of their primary parasites (Smith & Compere 1931; Flanders 1940; Burks 1979).

Among the other pteromalids the *Panstenon oxylus* (Panstenoninae) behaves as a predator on the eggs of *Javesella pellucida* whereas *Peridesmia discus* (Pteromalinae) plunders on the eggs of weevils *Phytonomus posticus*. The consumption of such eggs that have been laid separately (not in cocoons or under the cover of the eggs owner) is undoubtedly a new complication of biology, originating most likely from predatory activity on a group of secretively laid eggs.

As to other pteromalid links with insects eggs it can be said that the *Pachyneuron solitarium*, *Acroclisoides emeljanovi* and *Trichomalopsis redivii* which develop inside the egg shell are secondary parasites on the larvae of primary endoparasites of Lepidoptera and Hemiptera eggs. It may be surmised that they have passed to parasitism on larvae in eggs as a morphotypical specialization type (Kozlov 1970, 1972) which can be seen in Hymenoptera little cocoons or in the mummies of aphides.

One of the particularities in the pteromalid parasitism evolution of the koinobiontic direction is the unusual type of parasitism, accompanied by hypermetamorphosis. It developed in pteromalids of subfamily Chrysolampinae. A special feature of this type of parasitism is the presence of a mobile larva of the first instar, which independently finds a host within the limits of its refuge and gets into direct contact with him. Such a larva is called planidium; it was studied among species of genus *Chrysolampus* (Askew 1979; Darling & Miller 1991). In case of a development with hypermetamorphosis the female chalcidoid wasp does not lay its eggs directly on the host, rather at some distance from it. Having found the host and attached itself to it, such a larva becomes

paucimobile. It does not cause appreciable damage to the host – the larva of the third age of the beetle; that is why this last is still able to leave its refuge and escape to the ground in order to build there an earth cell for the pupation. After having constructed the earthen cell, the larva becomes immobile and undergoes histolysis. It is just to this moment that the recommencement of activity among chalcidoid wasps first instar larvae is timed, as well as the beginning of their feeding (Darling & Miller 1991). In evaluating the general sense and sequences of this line of biological evolution it should be born in mind that it is not the female chalcidoid wasp who gets into direct contact with the host, but the first instar larva. The laying of eggs by the female parasitic wasp at a certain distance from the host instead of directly on it inevitably leads to increasing mortality risk in case of unsuccessful host search. Accordingly, while being characterized by a relatively high general level of specialization, this type of parasitism evidently, represents itself the most primitive variant of koinobiontic parasitism, namely, koinobiontic ectoparasitism.

Chalcidoids and, particularly, pteromalids, are small insects for whom the possibility of transition of larvae from inhabiting inside the host instead of on it, that is, to a liquid medium from an aerial one, does not represent itself an insurmountable obstacle, as respiration may be exercised to a sufficient extent by the body surface (Tobias 1967). Just as in braconid parasitoids in this way the transition to endoparasitism emerged over and over again (Tobias 1967; Shaw 1983), so in pteromalids to all appearance, the same scene took place. The cases of endoparasitism in the same genera where ectoparasites are indicated, as for example in genera *Pteromalus*, *Stenomalina* or in closely related genera (*Triapitzinia*, *Psychophagus*, *Erdoesina*, *Stichocrepis*), are evidence of this.

Idiobiontic endoparasitism is regarded nowadays as the most primitive level of endoparasitism. Among pteromalids it has developed in Lepidoptera pupae and in cryptically dwelling larvae of some Diptera. It must be added that endoparasitism in overtly disposed pupae appears to have originated from endoparasitism in cryptically disposed pupae, as it has been with sufficient exactness traced among Ichneumonids (Gauld 1988; Kasparyan 1996). What concerns the relation of pteromalids with Diptera, it should be noted that *Stenomalina liparae* (Pteromalinae) develops endoparasitically in *Lipara lucens* larvae (Chloropidae) in galls on the common reed *Phragmites communis*. The endoparasitism of Diptera, in all likelihood, must be derived from ectoparasites of cryptobiontic Diptera larvae. The frequency of occurrence of both within the same genus, as it is observed, for example, in genera *Stenomalina* and *Sphegigaster*, is an argument that speaks in favour of this way of evolution.

On the whole both endoparasitism and ectoparasitism on overt hosts are secondary for pteromalids. It is not out of here to mention that endoparasites of overtly situated pupae of insects are relatively infrequent among pteromalids. These are mainly endoparasites of Lepidoptera pupae. But primary parasites of overtly living insect larvae are especially rare.

The koinobiontic trend in the evolution of pteromalids parasitism was realized in larvae – pupae parasites. This type of parasitism is widely represented between miscogasterines, which develop on leaf – miners from family Agromyzidae (Diptera). Notwithstanding the conservation of a primitive mode of infestation (through the substrate), these pteromalids are already highly specialized. A striking instance of the achieved degree of specialization may be the mode of life of *Halticoptera patellana* (Dalman) (Askew 1968). The female of this species lays its only egg into the adult larva of the fly without paralyzing it. Nevertheless the host larva develops normally up until the formation of the puparium in the soil. The first instar larva of the parasitic wasp gets out from the egg only in the host's puparium and sets about to intensive developing. Naturally, in the puparium the offspring of the pteromalid can be protected more securely. The preference of the evolutionary

path selected by the larvae – pupae parasites consists not only in the advantage that their females are delivered from the necessity of searching the puparia in the ground what it is not so simple in itself but also of the particularity that the parasitic wasp avoids competition with species that infest puparia.

The problem of the origin of endoparasitism in adult bark beetles among pteromalids of genus *Tomicobia* (Pteromalinae) is the most difficult for solution. It's an example of aggressive behaviour of a female parasitic wasp which infests a mobile host in direct contact. The female lays eggs into the body of the beetle without preliminary paralyzation (koinobiontic endoparasitism).

In braconid wasps, where parasitism on the adult stage has been observed too, the way of the transition from parasitism in Chrysomelidae beetles larvae to imago of these insects living in the same microstations is shown (Tobias 1965, 1966). A clear transition to adult parasitism of such kind has not been observed in pteromalids. However, we must admit that to all probability it is not a mere chance the fact that the representatives of other genera related to *Tomicobia* are linked with xylophagous beetles larvae. It would be permissible to suppose that within the limits of this ecological niche a change from ectoparasitism to endoparasitism in the larvae of the beetles has taken place, and then in the adult xylophagous beetles.

In the family Pteromalidae another direction of biological evolution is known, namely, secondary phytophagy. It has been veridically established in the Palaearctic region for *Blascoa ephedrae* Askew (Miscogasterinae) (Askew & Blasco-Zumeta 1997, 2000). Besides that, in the literature indications that the Palaearctic species *Mesopolobus nobilis* Walker (Pteromalinae) is a phytophagous one are met with (Zerova & Seryogina 1994). The authors cite Rosen's article (Rosen v. 1962). Incidentally Rosen himself only supposes the presence of phytophagy in this species. Phytophagous Pteromalids have been observed as well in South Africa, North America, Indonesia and Australia (Riek 1962; Bouček 1988).

Conclusions

It is clear that the present analysis does not represent an exhaustive explanation of the contents of parasitism evolution among pteromalids. Moreover the insufficiency of material and facts inevitably leads to a certain arbitrariness of analytical assumptions. However the afore mentioned arguments would be sufficient to make sure that in spite of the great diversity of methods of host utilization by pteromalids, they reflect two main trends in parasitism evolution of pteromalids, namely, idiobiontic and koinobiontic.

The idiobiontic direction with an obvious predominance of idiobiontic ectoparasites represents itself the main trend in the evolution of parasitism among pteromalids. It was realized not only in the subfamily Pteromalinae – the most numerous in the family – but in the majority of the other subfamilies as well.

The koinobiontic direction is represented in a considerably less pronounced way with a predominance of koinobiontic endoparasites. The transition to koinobiontic parasitism took place in several subfamilies; the most expressive example of this way of parasitism evolution was realized in the subfamily Miscogasterinae.

Nevertheless, in comparison with other Chalcidoidea families, such as Eulophidae and Encyrtidae, which possess a rather more significantly marked level of morpho-biological specialization, only the initial stages of koinobiosis formation and development take place.

A very important role in the evolutionary aspect was also played by the change to hyperparasitism. This evolutionary event should be regarded as a strategy for the assimilation of new adaptive zones. As a consequence, a further intensification of speciation processes in the family took place.

On the whole all the trends of biological evolution of pteromalids discussed here ensured them biological progress evidenced by their universal spreading, as well as their great taxonomic diversity on the level of subfamilies, genera and species.

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A NEW FAMILY OF THE MOST PRIMITIVE PARASITIC ACULEATE (HYMENOPTERA: ACULEATA)

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Abstract – New family Kislevidae established and illustrated. The representative genus *Kisleva*, with a subfossil species *Kisleva ohalona*, based on characteristics of head remnant, discovered in Israel, are described and compared with putative relatives.

Key words: Hymenoptera; Kislevidae; new; *Kisleva*; discovery; distribution; diagnosis

Introduction

Recent discovery of an extinct scolybythid from Lebanese amber (Prentice *et al.* 1996), of Early Cretaceous age (135–120 million years old), connected to genus *Ycaploca*, which I have described from South Africa and Australia, demonstrates that fauna of the Middle East still holds surprises.

The purpose of this note is to reveal in this area an additional new family, Kislevidae. The subfossil species *ohalona* in genus *Kisleva* are described, based on the uniqueness of a head remnant, and comparison with putative relatives. *Kisleva* appears to be one of the primitive aculeate wasps that lived parasitically in tree trunks. Its ventral placement of oral cavity and existence of genal furrow, for reception of resting antenna, are both indications that the species inhabited relatively constrained galleries of wood-boring insects, filled with sawdust and excrements. Its peculiar head combines together morphological characters, several of which are exclusive to families Megalodontidae, Megaloridae, Orussidae, Paroryssidae or Tiphidae. However, the genus possessing the largest number of comparable character state polarities, an evident sister-group of *Kisleva*, is the tiphid genus *Silifka*. The subfamily Silifkinae of Tiphidae described from Turkey, is a Laurasian relic from the Tertiary era.

Materials and Methods

The type material is a head remnant of a subfossil wasp, discovered in a prehistoric human settlement from the Great Glaciations period; not an inclusion from a specific geological stratum, only somewhat carbonized piece. The excavation site is located a few hundred meters from Sea of Galilee shore, designated Locus no. I of Ohalo II, situated westward from the southernmost corner of the lake. Revealed by the palaeobotanic research group lead by Professor M. Kislev, of Bar Ilan University, Ramat Gan. The accretion is estimated at 19,300 years old, prior to the present age. Confident dating, achieved through C14 radiocarbon detection methods, by isotope decay rate and particle extinction measurements (Nadel *et al.* 1995). It was disclosed concurrently with unrevealed fragments of a larva and pupa. Illustrative information presented here was drawn from photographs

taken with electron scanning microscope from a gold-coated specimen. In fact, two remnants were discovered. First from Pleistocene geological period, detailed below. Another genus and species come from the Byzantine historical period. It is a true bethylid and will be described elsewhere.

Results

Kislevidae fam. n.

Established with one genus and species, from the East Mediterranean Coast or Levantine zoogeographic sub-region. Main characters of the family are those of the described species.

***Kisleva* Argaman, gen. nov.**

Type-species. *Kisleva ohalona*, new species, by monotypy and by present designation.

Etymology. Dedicated to Prof. M. Kislev, organizer and director of the undertaking. Gender: feminine.

***Kisleva ohalona* Argaman, sp. nov.**

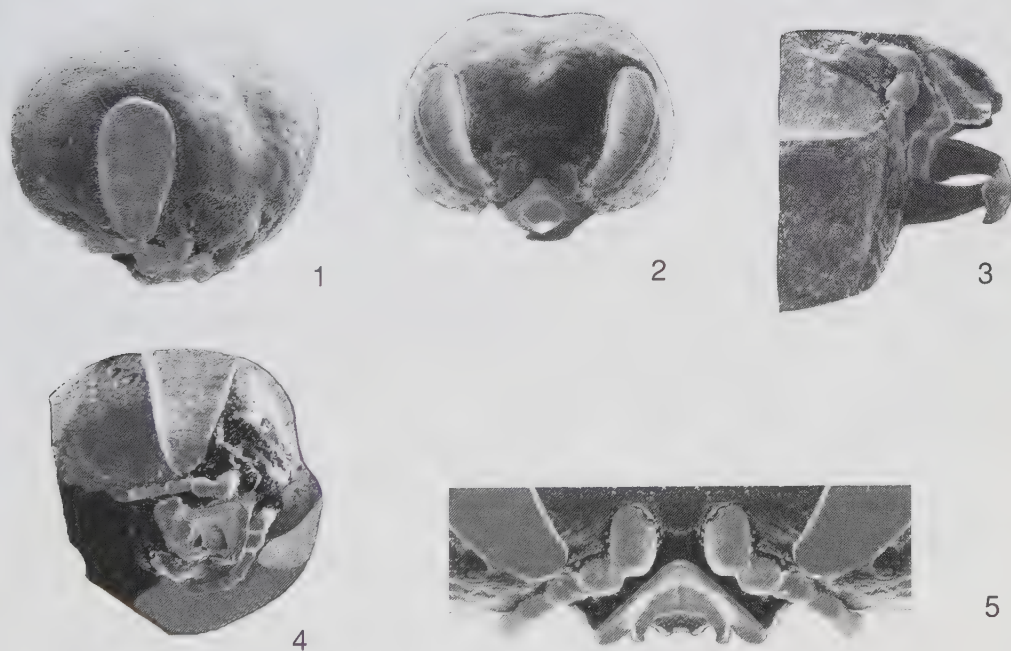
(Figs 1–5)

Type material. Holotype, subfossil head. From Locus No.1, Ohalo II excavation site, Galilee, Israel. Preparation #219, presently gold-coated. Type deposited at Department of Life Sciences, Bar Ilan University, Ramat Gan.

Description. Small wasps, of presumed body length 3 mm. Width of head about 0.9 mm. Head bulky, roughly two times as wide in frontal view as long in lateral view. Shape more or less oval in outline, with clearly incrassate temples. Eyes placed entirely on frontal aspect, rather elongated reniform in shape, three times as long as maximum width; ommatidia distinct, clothed with fairly long, scattered pubescence; hairs about half as long as major width of an eye. Outer orbit convex, evenly arched; inner orbit more deeply concave, particularly along lower half of front; both orbits obviously converging downward; width of an eye at upper third about twice the width at lower third. Overall contour of head roughly hemispherical in lateral view, vertex evenly curved into frons; everywhere convex, except upper frons bears broad and shallow longitudinal concavity. Ocelli small, nearer to eye orbit than distance connecting them; front angle of ocellar triangle obtuse-angled; width of ocellar triangle four times ocello-ocular line. Temples in lateral view of head two times as long as maximum width of an eye. Occipital margin straight, truncate. Occiput not margined by carina, post-occipital ridge blunt. Antennal toruli located on lowermost margin of face, between inner eye orbits and supraclypeal triangle, separated from fronto-clypeal suture of upper clypeus by their own major diameter. Toruli bordered by a minute, delicate ring, but are neither tuberculate nor covered by a protruding frontal emergence from above. In normal posture of head, the antennal insertion is placed somewhat above lowermost boundary of head. Antenna incomplete, only six basal segments retained. Scape one and half times as long as wide, its ventral margin straight, dorsal boundary moderately arched. Pedicellus subglobular in outline, as long as wide. First four flagellar segments cylindrical, about as wide as long or slightly longer. Whole

postgena along outer margin of proboscideal fossa moderately deeply impressed, forming a longitudinal furrow below lower eye margin, about as deep as width of antenna. Antenna relocated into this furrow at rest. Supraclypeal area trapezoidal and protruding between antennal toruli above. Upper clypeal lobe deeply emarginated, separated by strong lateral crest from malar space. The crest initially forms triangular lobe ventro-laterally, then becomes abruptly declivous and projected backward below the mandibles, joining paramandibular process of hypostome. Lower clypeal lobe narrow stripe with almost flat dorsal surface, also obviously emarginated deeply, horseshoe-shaped. Labrum slightly convex, semicircular in outline, bluntly bituberculated apically. General posture of head orthognathous, as entire oral area situated on its ventral aspect. Mandibles moderately wide, parallel-sided, flattened; the widest plane parallel to longitudinal axis of body; separated from clypeus by their own width; moderately overlapping at rest, but not intercrossing; hold bidentate apices. Apparent palpal formula 3–5, but the eventual existence of rather small basal, labial or maxillary palpal segment cannot be excluded.

Biology. Not too much known about the habits of this species. Shape of head indicates that it inhabited relatively limited galleries of wood-boring insects, filed with sawdust and excrement. Estimation is supported by placement of oral cavity and existence of genal furrow of antenna at rest. Since true woodborers, Scolytidae, Platypodidae or Bostrichidae (Coleoptera), possess the same ground-plan trait of head, i.e. oral cavity retracted under carapace. Although head surface of



Figures 1–5 *Kislewa ohalona* gen. nov. & sp. nov. 1, head, sublateral aspect; 2, head, frontal and slightly subventral aspect; 3, clypeal region, sub-lateral aspect; 4, head and oral cavity, ventral aspect; 5, Clypeal region, viewed from above

the majority of wood inhabiting hymenopterans are equipped with secondary adaptive patterns, such as protuberances, crests or adorbital sharply foveolate carinae (various stephanids, orussids, megalyrids, eupelmids), there are many groups without.

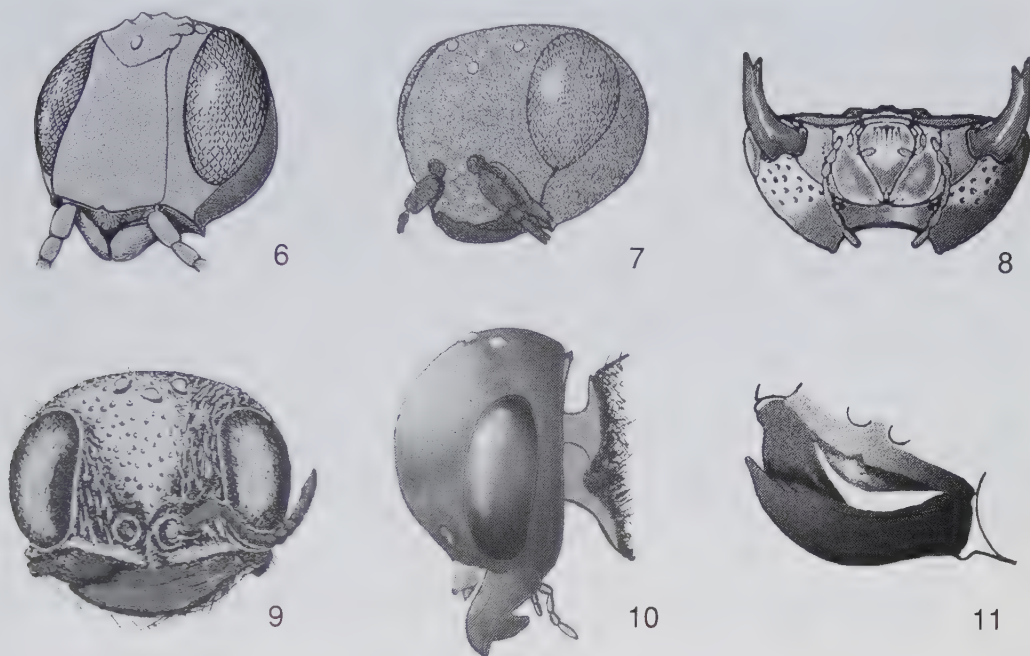
Discussion

The bulky head of *Kisleva*, with down converging eye contour and inner eye orbits obviously narrowed ventrally, are unique characters within Hymenoptera. Placement of flattened mandibles along longitudinal axis of body is also exceptional. In most of contemporaneous hymenopterans, the frontal plane of mandibles is vertical, respectively transversal to the longitudinal axis. Hence no any other species is known with so sharply carinulated paramandibular process or so remotely distant mandibles from posterior aspect of the clypeus. Cavity of resting antenna of *Kisleva* is a shallow, insignificant impression on malar space, produced in a genuine furrow on latero-ventral aspect of head. Closely reminiscent of, and almost certainly homologous with, the remarkable antennal cavity of megalyrids and orussids. In these families, however, it is developed obliquely on the face (Fig. 7) or is addition to a crest-like lower front, almost covering the antennal toruli above (Fig. 6). Such a feature not developed in *Kisleva*. Assembly of these character states indicates that genus *Kisleva* belongs to a family of its own. Head of *Paroryssus extensus* likewise bulky, but inner eye orbits are uniformly convex.

Cavity of resting antenna underneath lower eye margin in Kislevidae is a character that occurs only within Paroryssidae, Megalyridae and Orussidae. Paroryssidae is extinct at present, contains three fossil genera, *Paroryssus*, *Microryssus* and *Praeoryssus*, disclosed from the Late Jurassic of a southern Kazakhstan excavation site (Rasnitsyn 1968). As the paramandibular process of these fossils could not be ascertained, a comparison is not possible. All contemporaneous members of the other two families examined, megalyrids and orussids, possess no trace of a paramandibular process. There exist apparently only four possible developmental states of the paramandibular process within the Order Hymenoptera (Richards 1956: Fig. 12):

1. In a primitive state, broad bridge of hypostome reaches and actually fuses posterior aspect of clypeus, entirely enclosing mandibular articulation inwardly (Fig. 8).
2. In a derived state, having same conformation as above, but not actually reaching clypeus, separated from it by a small hollow.
3. In a moderately advanced state, reduced to a narrow septum of proboscoidal fossa, not quite touching the clypeus posterad.
4. In a completely advanced state, paramandibular process not developed at all.

Plesiomorphous condition (1) occurs within Megalodontidae, Bethyridae (Pristocerine males), Tiphidae (both sexes), Myzinidae (Meriinae females), Methocidae (both sexes, only in female of Pterombrinae), Mutillidae (Myrmillinae females, Pseudophotopsidinae males), Anthoboscidae (in females), Ampulicidae (both sexes of Ampulicinae, none of Dolichurinae), Apoidea (*Anthophora* females, *Chalicodoma* males, *Nomada* and *Halictus* females). All are relatively primitive groups, an evaluation based on morphological or narrowed paramandibular process are characteristic of



Figures 6–11 Comparative head profiles of Hymenoptera: 6, *Guiglia* sp. (Orussidae), sub-lateral view; 7, *Megalyra* sp. (Megalyridae), the same (redrawn after Riek 1970); 8, Generalized *Tiphia* head (Tiphidae), ventral aspect, showing the large paramandibular process. 9–11, *Silifka fatima* (Tiphidae), 9, frontal aspect, 10, lateral aspect, 11, clypeal region in sublateral view

Scoliidae (females), some genera of Apoidea (*Ceratina*), and Sphecoidea (*Auchenophorus*, *Parapiagetia*, Philanthinae, Sphecinae). However, I failed to detect any trace of development of paramandibular process in cephids, tenthredinids, trigonalids, ichneumonids, cleptids, chrysidids, rhopalosomatids, pompilids, formicids, masarids, eumenids, vespids or most *Xylocopa* examined. Since a complete paramandibular process accompanies relatively primitive character states, it is a strong plesiomorphy and not a minor adaptive advancement as stated by Bohart & Menke (1976).

Among symphyta, most distinct are Megalodontidea. Characterized by hypertrophied cutting mandibles and union of clypeus and hypostome via solid paramandibular process. Since every group owning a paramandibular process is primitive, archaic parentage of megalodontids is automatically inferred. Königsmann (1977) and Rasnitsyn (1979) overwhelmingly documented that Xyelidae is the most archaic representative and parent of Symphyta. According to their view, all further fossil or contemporaneous families of Hymenoptera developed from a prehistoric xyelid. Megalodontids are web makers or leaf rollers; xyelyds are pollen-feeders. In theory, megalodontids could have evolved during Silurian or Devonian, simultaneously with ancient vascular cryptogams. In contrast, xyelids only in Carboniferous, together with pollen producing phanerogams. For all these reasons, I consider Megalodontidae, and not Xyelidae, to be the ancestral group.

Within aculeates, only *Silifka* Argaman & Özbek possesses both a paramandibular process and transversely divided clypeus (Figs 9–11). In others, upper clypeus either constricted in a medial longitudinal crest, as all bethylids, excepting male of '*Afrisobrachium*' *babaeculuscum* Benoit, or sharply compressed in a protruding dentiform tubercle as in *Cerceris* and some thynnids. Clypeal separation completely disappear in cleptids, chrysidids, pompilids, formicids or vespids. In plus, in *Kisleva* antennal toruli situated very low on face, touching fronto-clypeal suture. It is similarly a strong plesiomorphy, since this is the ground-plan character state of bethylids, tiphiids, scoliids and mutillids. In advanced families, antennal torulus separated from fronto-clypeal suture by its own major diameter or more. Transversely divided clypeus of both *Kisleva* and *Silifka* is homologous with post-clypeus and ante-clypeus of *Corydalis* (Megaloptera) and *Wesmaelius* (Neuroptera). Uniquely within hymenopterans, these two genera reveal one of the strongest plesiomorphous character states. Nevertheless, *Kisleva* is not tiphiid. Among the most primitive aculeate wasps, deeply emarginated clypeal disc occurs only within Scolebythidae and in sclerodermines of the Bethyridae. Both of them live parasitically on woodborers. It seems that Kislevidae is an ancestor of these. In conclusion, placement of Kislevidae among most primitive aculeate hymenopterans is a matter of subjective assessment and was influenced, among other things, by the personal impressions of the author.

Acknowledgements

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PSEUDOCLERUCHUS TRICLAVATUS DONEV AND HUBER, GEN. AND SP. NOV. (HYMENOPTERA: MYMARIDAE), WITH NOTES ON THE CLERUCHUS-GROUP OF GENERA

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Abstract – *Pseudocleruchus triclavatus* Donev and Huber, **gen. nov.** and **sp. nov.**, is described from six females collected in the Rodopi Mountains and Stara planina ridge, Bulgaria. This genus is in a group of nine genera, informally named the *Cleruchus* group. *Platypatasson*, **syn. nov.** is removed from synonymy under *Cleruchus* and synonymized instead under *Platystethynium*. Its type-species is transferred as *Platystethynium fransseni* (Ogloblin), **comb. nov.**

Key words: Mymaridae, *Pseudocleruchus*, *P. triclavatus*, new genus, *Cleruchus* group

Introduction

The new genus described below belongs to a group of at least eight other, related genera, treated informally here as the *Cleruchus* group: *Apoxipteron* Noyes & Valentine, *Ceratanaphes* Noyes & Valentine, *Cleruchus* Enock, *Eucleruchus* Ogloblin, *Haplochaeta* Noyes & Valentine, *Platystethynium* Ogloblin, *Prionaphes* Hincks, and *Paracmotemnus* Noyes and Valentine.

The *Cleruchus* group cannot be defined by the common possession of any single feature, but by a combination of features, any one of which may not occur in all the genera. These features identifying the group include: face usually angular in lateral view, strongly receding below toruli to mouth; stigmal vein often widened, sometimes wider than long; funicle segments of females usually subquadrate or wider than long; mesosoma often somewhat flattened, wider than high; forewing usually narrow and often parallel sided; and legs often short and stout.

The southern hemisphere is clearly the present centre of diversity for the *Cleruchus* group. Except for the cosmopolitan *Cleruchus* the remaining described genera occur south of the equator or in equatorial regions. *Ceratanaphes* occurs in Australia and New Zealand (Noyes & Valentine 1989) and was recently found in Chile (2 females, Canadian National Collection, Ottawa). A Baltic amber fossil (Jens Janzen private collection, Seevetal, Germany) indicates that *Ceratanaphes* once occurred in the northern Hemisphere as well. *Apoxipteron*, *Haplochaeta*, and *Prionaphes* are known only from New Zealand, and *Paracmotemnus* occurs in New Zealand and Australia (Noyes & Valentine 1989). *Eucleruchus* is known from Argentina (Ogloblin 1940) and *Platystethynium* is known from Indonesia (Ogloblin 1946). The past occurrence of *Ceratanaphes* in the northern hemisphere indicates that its current Gondwanan distribution is relictual; the genus has gone extinct elsewhere.

Ogloblin (1946) pointed out what he considered the remarkable parallelism of features in his *Platystethynium* and *Platypatasson*, which he attributed to convergence caused by adaptation to parasitism in eggs of Tettigonoidea. Members of both genera were reared from the same locality in Java and possibly from the same host, a "locustid" (= Tettigoniidae, not Acrididae as stated by Schauff 1984). Ogloblin treated his genera as being related to other, quite different genera: *Platystethynium* to *Stethynium* and *Platypatasson* to *Patasson* (now a species group in *Anaphes*), respectively, based presumably upon the different number of claval segments in females (three in the first two genera and two in the second two genera). The number of claval segments in females is known to vary among species of the same genus, e.g., *Prionaphes* and *Stethynium* (Noyes & Valentine 1989). Flagellomere number in males of *Cleruchus* also varies (Debauche 1948). We agree with Noyes and Valentine that claval segmentation is a poor character for defining genera. Because almost all the other features of *Platystethynium* and *Platypatasson* females are the same we consider that their features are not convergent but were inherited from a common ancestor and that the two taxa form only one genus. Schauff (1984) had synonymized *Platyptasson* under *Cleruchus* but we remove it from synonymy under *Cleruchus* and instead synonymize *Platypatasson* under *Platystethynium*, **syn. nov.** *Platypatasson fransseni* Ogloblin is transferred to *Platystethynium*, **comb. nov.** Males of *Platypatasson* have rudimentary wings (Subba Rao 1970). When males of *Platystethynium onomarchicidum* Ogloblin are discovered and compared with those of *P. fransseni* the synonymy proposed here may be better confirmed.

Methods

Two of the six known specimens of *Pseudocleruchus* were slide-mounted in Canada balsam, without clearing in KOH. The remainder are in alcohol or critical point dried and card-mounted. All measurements are in micrometers, unless given as ratios. Holotype measurements are given first followed by one paratype measurements in parentheses, where available. Abbreviations used are fu, for funicle segment, Gt, for gastral tergum.

Pseudocleruchus Donev and Huber, gen nov.

Type species: *Pseudocleruchus triclavatus* Donev and Huber, **sp. nov.**

Diagnosis. Females of *Pseudocleruchus* differs from those of *Cleruchus* by the following features: clava (Figs 4, 8) 3-segmented (1-segmented in *Cleruchus*); radicle fused with scape (distinctly separated in *Cleruchus*); ocellar triangle relatively high (Fig. 1), with OOL about half POL and posterior ocellus separated by about 1.5 X its diameter from supraorbital trabecula (ocellar triangle low, with OOL much less than half POL and posterior ocellus almost touching supraorbital trabecula in *Cleruchus*); stemmaticum trapezoidal and indicated by pale markings (stemmaticum elliptical and indicated by sutures in *Cleruchus*); mandibles reduced, not meeting medially (overlapping medially in *Cleruchus*); prosternum entire (longitudinally divided in *Cleruchus*); stigmal vein (Fig. 5) not wider than marginal vein (distinctly wider in *Cleruchus*); forewing (Fig. 6) not parallel-sided and with relatively numerous microtrichia (parallel sided and with few microtrichia in *Cleruchus*); mesophragma (Figs 2, 7) extending into gaster and weakly bilobed apically (mesophragma not extending past petiole and rounded apically in *Cleruchus*);

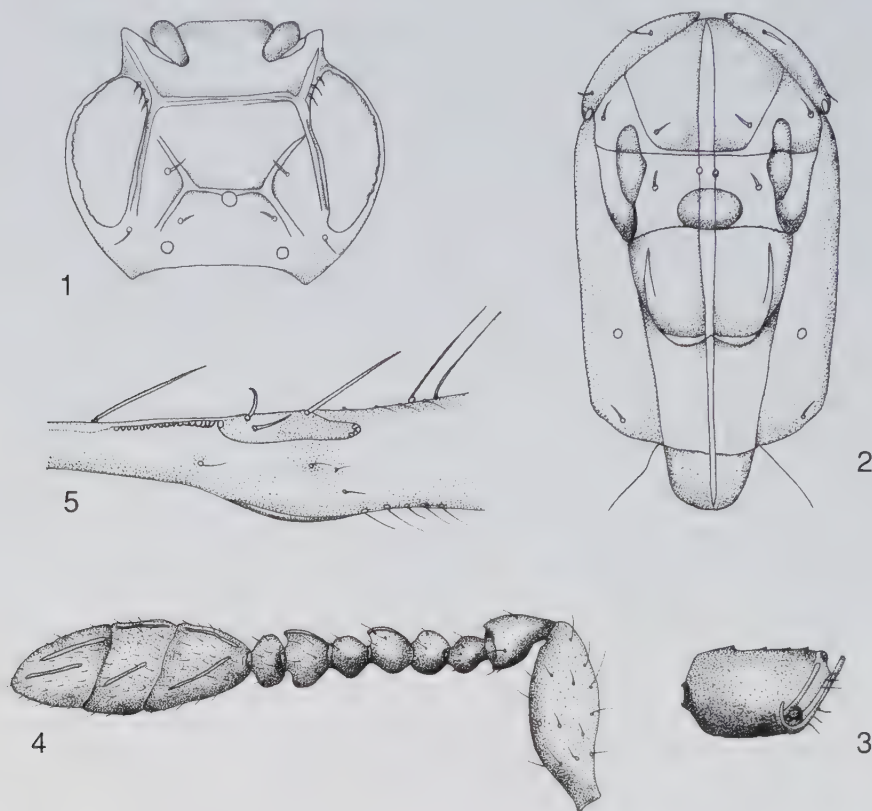
petiole indistinct (Fig. 3) not abruptly narrower than gaster (petiole distinct and abruptly narrower than gaster in *Cleruchus*).

Pseudocleruchus is most similar to *Eucleruchus*. Both have the radicle not separated from the scape, entire supraorbital trabecula, marginal vein not widened, and an indistinct petiole with the mesophragma extending into the gaster. In contrast, *Eucleruchus* has an entire clava and the prosternum is longitudinally divided.

Description. Female. Head (Figs 1, 7) in dorsal view about 1.2 X as wide as long, slightly wider than mesosoma (165:152), in lateral view triangular, with face strongly angular and receding sharply below toruli towards mouth. Face with subantennal groove extending from each torulus to mouth margin, with a pointed protruberance at apex of transverse trabecula between torulus and eye, and with 1 and 1 setae between toruli, 2 and 2 setae below toruli sublaterally, and 2 and 2 setae along lateral sulcus separating face from gena. Malar space with 1 seta near lateral sulcus of face. Toruli separated from transverse trabecula by slightly more than half their own length. Vertex (Fig. 1) with stemmaticum present as trapezoidal arrangement of white lines around ocelli and a line extending from each anterior corner of trapezoid toward junction of transverse and supraorbital trabecula, and with 3 and 3 sublateral setae, 1 and 1 behind lateral ocelli, 1 and 1 inside stemmaticum lateral to median ocelli, and 1 and 1 outside stemmaticum anterior to median ocellus; POL:LOL:OOL = 51:28:26; distance from median ocellus to transverse trabecula about 4.4 X median ocellar length. Supraorbital trabecula entire. Dorsal orbit with 4 setae, 1 posteriorly and 3 anteriorly. Eye with a few scattered short setae among ommatidia. Temple in dorsal view about 0.26 X width of eye. Occipital margin in dorsal view slightly curved inward, its anteriormost point almost in line with line connecting posterior ocelli. Gena with 3 setae behind eye. Antenna (Fig. 4) about 0.6 X body length, with radicle not separated from scape, with 6 more or less quadrate funicle segments, and with 3-segmented clava. Mandibles small, not meeting medially, each with a single pointed tooth and one apparently with a small blunt ventral (posterior) tooth.

Mesosoma (Figs 2, 7) not flattened dorsoventrally. Pronotum visible in dorsal view, about 0.14 X as long as mesoscutum along midline, divided into two lobes abutting medially, each lobe with 2 setae dorsally. Propleura meeting medially, each with 1 seta on inner margin. Prosternum not longitudinally divided, with anterior margin broadly rounded, and with 1 and 1 setae in posterior half. Spiracle oval, flat, at extreme posterior apex of pronotal lobe. Mesoscutum 1.6 X as broad as long (148: 78), with straight, percurrent notauli, with 1 and 1 setae in posterior half of midlobe, and with 1 seta at posterolateral angle of each lateral lobe. Scutellum about 1.4 X as long as mesoscutum; anterior scutellum more than half as long as posterior scutellum (43:69), with the two placoid sensilla in anterior half separated from each other by about twice their diameter, and with 2 sublateral seta. Axilla with a minute seta on inner margin of lateral panel. Posterior scutellum slightly wider medially than anteriorly and distinctly bilobed posteriorly. Metanotum scarcely visible laterally and not visible medially, with 1 minute seta submedially on each lateral panel. Mesophragma narrowing gradually, extending into metasoma just past base of Gt_1 , and weakly bilobed at apex. Propodeum about twice as long as scutellum (113:59); propodeal seta close to posterior margin.

Wings. Forewing (Fig. 6) slightly shorter than body length, with anterior and posterior margins not parallel; discal setae numerous and evenly distributed beyond venation, sparse behind venation; longest marginal cilia slightly longer than greatest wing width. Venation (Fig. 5) 0.37 X wing length; submarginal vein with 17–20 bullae; marginal vein with hypochaeta basal to proximal macrochaeta and distal macrochaeta distinctly longer than proximal macrochaeta.



Figures 1–5 *Pseudocleruchus triclavatus*, holotype and paratype. 1, head, dorsal view; 2, mesosoma, dorsal view, showing mediolongitudinal gap (separating dorso-longitudinal muscles) and oval area of thin cuticle behind placoid sensilla (indicating location of heart); 3, gaster (paratype); 4, antenna; 5, forewing base

Hindwing with 1 row of microtrichia between the usual anterior and posterior rows and a partial second row medially; longest marginal cilia about 2.6 X wing width. Venation about 0.34 X wing length.

Legs. Relatively short and robust (Fig. 7), with tarsi 4-segmented. Foretibial spur forked apically, with outer tine more than 2 X as long as inner tine.

Metasoma. Petiole short, scarcely visible. Metasoma (Fig. 3) oval in dorsal view, with posterior margin of each tergum straight. Gastral spiracle absent. Cerci oval with 4 setae, the longest extending to apex of ovipositor. Ovipositor about 1.2 X as long as hind tibia.

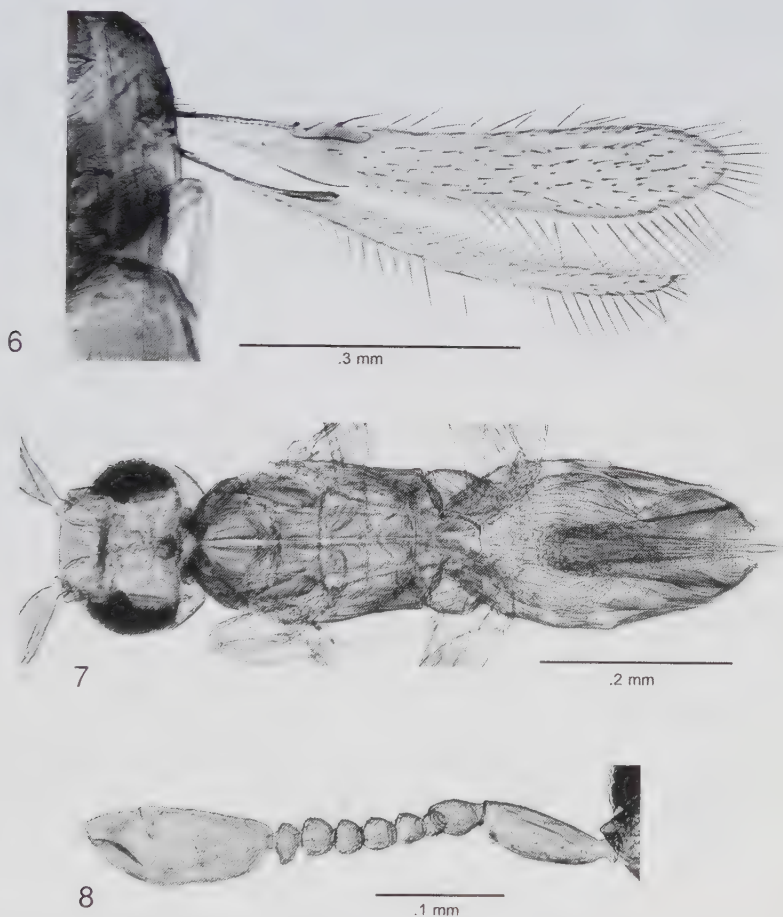
Male. Unknown.

Etymology. The genus is named from Greek “pseudos” meaning false, and *Cleruchus*. Gender masculine.

Pseudocleruchus triclavatus Donev and Huber, sp. nov.

(Figs 1–8)

Type material. **Holotype** female #61537, mounted in dorsal view on slide in Canada balsam and labelled: 1."26.VI.1999 m[ountain] h[otel] Martsiganitsa Rodopi Mts. 1470m, Bulgaria leg. A. Stoyanova". 2."Pseudocleruchus triclavatus det. Donev et Huber". **Paratypes.** Bulgaria: Stara planina ridge, 25.VI.1996, 1050 m, leg. A. Donev #61537 (1& on slide); Rodopi Mts., Pamporovo, 30.VII.2000, leg. A. Stoyanova" (3&& in alcohol and 1 on card). The holotype and 3 paratypes are deposited in the collection of the Department of Zoology, University of Plovdiv, Bulgaria, and one card-mounted paratype is in the Canadian National Collection of Insects, Ottawa.



Figures 6–8 *Pseudocleruchus triclavatus*, holotype and paratype. 6, wings (paratype); 7, body, dorsal view; 8, antenna (fu_6 and clava from one antenna placed on clava- fu_5 of other antenna by digital imaging)

Description. Female. Coloration. Mesosoma and metasoma brown except Gt₃–Gt₅ each with transverse light brown band; head, antenna, coxae, and femora lighter brown, pronotum, propodeum, and ovipositor plate darker brown; tibiae and tarsi yellowish. Stemmaticum defined by pale lines in an H-like pattern in front of and lateral to ocelli. Wings slightly darkened, except for narrow clear band parallel to forewing margin in apical third.

Body 728 (683) long, without evident sculpture (body sculpture cannot be properly seen because the specimens are uncleaned).

Head (Fig. 1) 122 long. Antenna (Fig. 4) with length/width measurements as follows: scape 111/33, pedicel –/.28, fu₁– fu₆ 20/20, 25/24, 22/28, 25/27, .23/30, .18/32, clava 143/64 (claval segments 1–3: 50, 39, 54). Fu₁ and fu₂ quadrate, fu₃–fu₆ broader than long. Fu₃ and fu₅ each with one longitudinal sensillum; clava with 2 longitudinal sensilla on each of the first two segments and 3 on the third.

Mesosoma (Fig. 2) 250 long and 148 wide. Forewing (Fig. 6) 643 long, 103 wide, length/width about 6.3, microtrichia on blade uniformly distributed beyond stigmal vein; longest marginal cilia almost as long as greatest wing width. Hindwing (Fig. 6) 608 long, 31 wide, longest marginal cilia about 2.6 X greatest wing width. Leg measurements (holotype) as follows:

	Coxa	Trochanter	Femur	Tibia	Tarsus				
					Total	1	2	3	4
Foreleg	103	46	130	121	118	34	31	26	28
Middle leg	57	46	122	154	126	28	37	31	31
Hind leg	91	58	147	215	147	35	43	37	32

Metasoma (Figs 3, 7) 336 long, 172 wide. Petiole about 7 long; lengths of gastral terga Gt₁–Gt₆ (including Gt₇, which is not distinguishable): 20, 45, 44, 55, 62, 77; Gt_{3–5} with 2 and 2 sublateral setae, Gt₆ with 3 and 3 setae, and Gt₇ with 4 evenly spaced setae between cerci. Ovipositor 257 long, exerted about 0.13 X its length beyond apex of metasoma. Ovipositor plate (Gt₇) with 3 and 3 setae apically, and 3 and 3 setae submedially.

Specific epithet. From latin, *tres*, three, and *clava*, club, referring to the 3-segmented clava.

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A NEW *PLECTOCYNIPS* SPECIES (HYMENOPTERA: FIGITIDAE: THRASORINAE)

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Abstract – A new species of Thrasorinae (Cynipoidea: Figitidae) from Chile, *Plectocynips pilosus* sp. nov., reared from galls of *Nothofagus dombeyi*, is described. The type material of the only known species of this genus, *Plectocynips longicornis*, has been studied and the morphological differences between it and *P. pilosus* are described.

Key words: Hymenoptera, Cynipoidea, Figitidae, Thrasorinae, *Plectocynips*, *P. pilosus*

Introduction

The monotypic genus *Plectocynips* was proposed by Díaz (1976) based on *P. longicornis* Díaz, 1976. She placed *Plectocynips* within the subfamily Figitinae and he remarked that it resembles another monotypic genus *Thrasorus* Weld, 1944, with one known species, *T. pilosus* Weld, 1944, described from UK. Currently both genera are placed into subfamily Thrasorinae. (Ronquist 1999).

Kovalev (1994) proposed the family Thrasoridae for the figitid genus *Thrasorus*, but Ronquist (1999) considered it as a subfamily of Figitidae and included the following genera into Thrasorinae: *Euceroptres* Ashmead, 1896; *Thrasorus* Weld, 1944; *Myrtopsen* Ruebsaamen 1908; *Pegascynips* Brèthes 1928; *Plectocynips* Díaz 1976 and an undescribed genus (Ros-Farré & Pujade-Villar, *in prep*). This subfamily is characterized by having metacoxa distinctly inflated (according to Ronquist 1999). Little is known about the representatives of this subfamily because of the lack of collected and studied material. Although the biology of the Thrasorinae is practically unknown, it is known only that species of this subfamily are associated with cynipid and chalcid galls. They might be parasitoids of gall inducers or other Hymenoptera associated with galls. Also they might beinquilines in galls.

The genus *Plectocynips* and *Pegascynips* form a monophyletic group within the Thrasorinae because of the extremely long metatibial spur (Fig. 1a) (Ronquist 1999), and also because they have only one spur on the metatibia. According to our observations, in both genera the females have an extremely long 7th sternum in the metasoma (Fig. 1b). The main diagnostic differences between *Plectocynips* and *Pegascynips* are scutellar foveae well marked and the metasoma is strongly compressed in *Plectocynips* while in *Pegascynips* scutellar foveae absent and the metasoma is not compressed at all.

Brèthes (1928) mentioned that the propodeum in *Pegascynips* is very prolonged and metacoxa came out below it, but we could not checked this characteristic because the type material is not well preserved and thus we do not included this character for differentiation *Pegascynips* from *Plectocynips* moreover, our studies showed that the propodeum in *Plectocynips* is not so long.

Díaz (1976) gave another distinctive *Plectocynips* character: clypeo-pleurostomal lines are very deeply marked and they have a small fovea on the superior part and the epistomal sulcus goes from one foveae to other. This character has also been observed in *Plectocynips pilosus* **sp. nov.** (Fig. 1c), however, we do not know whether this character presents in *Pegascynips* also, but in the other Thrasorinae genera we already examined (*Myrtopsen* and an undescribed genus) this character is very noticeable. Finally, the 19-segmented antenna of *Plectocynips longicornis* male (Díaz 1976) could be a very good character to differentiate *Plectocynips* and *Pegascynips* from all other Thrasorinae genera, but males of *Pegascynips barahonai* Brèthes (1928) and *Plectocynips pilosus* **sp. nov.** are unknown yet.

Materials and Methods

Specimens of *Plectocynips pilosus* **sp. nov.** we have studied were reared from galls of *Nothophagus dombeyi* (Mirb.) (Fagaceae), and were loaned by the Natural History Museum of London. The type material of *Plectocynips longicornis* deposited at the 'Museo de la Plata' (Argentina) and *Pegascynips barahonai* deposited at the 'Museo Argentino de Ciencias Naturales' (Argentina) was also studied.

All the type material was examined either with SEM (without coating and under very low voltage to preserve specimens from damaging) or with stereomicroscopy (mounted on cardboards).

We follow the current terminology of morphological structures (Richards 1977; Ronquist & Nordlander 1989; Ronquist 1995; Ros-Farré *et al.* 2000), the surface sculpturing is given after Harris (1978). Abbreviations used here include: POD (post-ocellar distance) is the distance between the inner margins of the posterior ocelli; OOD (ocellar-ocular distance) is the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; COD is the distance between lateral and frontal (central) ocellus.

Plectocynips pilosus Ros-Farré, **sp. nov.**

(Figs 1, 2c, d)

Type material. Holotype female labelled "ex Cynip galls on *Nothophagus dombeyi* reared", "Chile: Parque Nacional Nahuelbuta II-III, 1985 Gauld". **Paratypes:** 4 females with the same labels as the holotype (all are deposited in The Natural History Museum of London (NHML), except 1 paratype female in the collection of the University of Barcelona, Spain (UB)).

Description. Female. Head, mesosoma and metasoma black; antennae brown, with lighter pedicellum; mandible and legs amber yellow.

Head (Fig. 1c) with dense and long white pubescence; gena not inflated and less pubescent, with very weak striae; occipital carina absent. Compound eye protruding laterally; malar space 0.5 times height of eye; malar field present but very superficial. Epistomal furrow weak but clear; pleurostomal lines inclined (confluent) and strongly marked, forming a deep furrow on each side of clypeus, which projected into a sheet, strongly curved marginally. Area between pleurostomal lines and compound eyes with striae, rest of face smooth. Transfacial line 1.3 times height of eye. Antennal foramina big, with prominent lip; area above antennal foramina shiny and glabrous; occiput smooth. POD:OOD:COD ratio as 5:3:2; maximum diameter of lateral ocellus is 2.

Antenna filiform, 13-segmented; scape and pedicel very pubescent internally and glabrous externally. Antennal formula: 5: 3: 5: 6: 5: 5: 4: 3.9: 3: 3: 3: 3: 4.

Mesosoma (Figs 1b, 2c & 2d) with dense and long pubescence; lateral surface of pronotum with few weak carinae; subpronotal plate projected. Mesoscutum nearly smooth, with weak xagrate sculpture on basal margin; 1.3 times as broad as long and 1.6 times as high as long; notauli complete and smooth interiorly, slightly broadened basally; median mesoscutal impression very weak and present only basally. Mesopleuron smooth and glabrous, with a transversal furrow in inferior 1/3. Scutellar foveae oblicuous, without pubescent interiorly, smooth; superficial in internal margin and getting deeper towards their external margin. Scutellar disc rugose. Distal margin of scutellum straight. Propodeal carinae complete, very conspicuous and curved, delimiting a xagrate and pubescent internal area.



Figure 1 *Plectocynips pilosus* Ros-Farré, **sp. nov.**: a, metatibial spur; b, female, lateral view; c, head, front view

Legs (Fig. 1a). Metatibial spur extremely long and curved.

Wings membrane pubescent and brownish; fore wing ciliate marginally; marginal cell closed, 2.7 times as long as wide; Rs+M blurred but clearly reach distal part of basal vein; areolet absent; R2 straight, 2r slightly curved.

Metasoma (Fig. 1b) petiole short and smooth. Third abdominal tergum with few hairs laterally, shorter than fourth, which occupy most part of metasoma. Ventral spine of hypopygium very short, 7th sternum very long and big.

Male. Unknown.

Etymology. The species is named “*pilosus*” because of the conspicuous pubescence that strongly differs it from other known species of the genus.

Discussion

There are some important diagnostic characters that differentiate *P. longicornis* (Fig. 2a) from the newly described *Plectocynips* species: *P. pilosus* (Figs 1b, 2b & 2c) has a very conspicuous and long pubescence covering all the body while *P. longicornis* (Fig. 2a) is covered with only few scattered hairs.

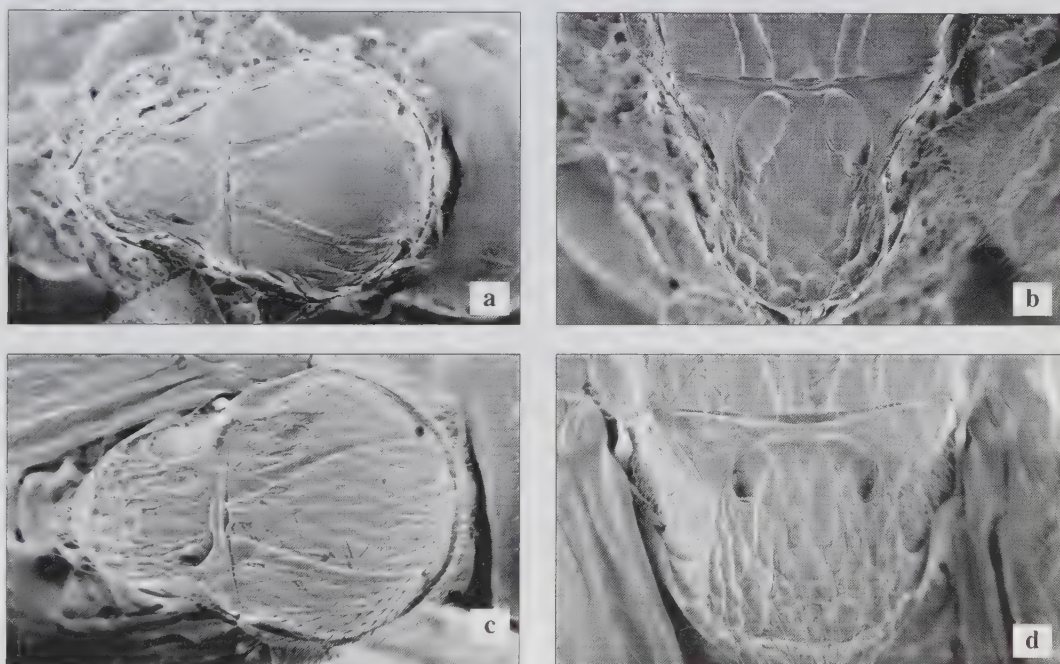


Figure 2 Mesosoma (a, c) and scutellum (b, d) in dorsal view: a, b, *Plectocynips longicornis*; c, d, *Plectocynips pilosus* Ros-Farré, **sp. nov.**

The scutellum (Fig. 2b) is rounded and rugose distally, scutellar foveae are large, very smooth and rather superficial in *P. longicornis*, while in *P. pilosus* (Fig. 2d) the scutellum is straight distally, with a rugose sculpture from the distal margin of the scutellar foveae to the end; scutellar foveae are small, deep and with some weak sculpture. Also the posterior part of the notaulices are a bit broader in *P. pilosus* (Fig. 2c) than they are in *P. longicornis* (Fig. 2a).

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ANDRICUS CATILLA (DARBOUX & HOUARD, 1907) IS A VALID SPECIES (HYMENOPTERA: CYNIPIDAE)

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Abstract — *Andricus catilla* (Darboux & Houard, 1907) known from its gall only, has been considered as a dubious species. We established its validity after studying the material from Giraud collection. The gall wasp is described and separated from *A. stefanii*, a species inducing similar galls. The lectotype of *A. catilla* and a neotype of *A. stefanii* are designated herein.

Key words: Cynipidae, *Andricus catilla*, *Andricus stefanii*, taxonomy, description

Introduction

The description of *Andricus catilla* has remained unnoticed for a long time. Darboux & Houard (1907) mentioned it for the first time as a possible new variety of *Andricus polycerus* (Giraud, 1859), without naming it, however stating that Giraud planned to give a new name to this gall: “*Cynips catilla*”. Colour plates of the gall, made under Giraud’s supervising were included in this work. Galls of this species were described again, with figures in Houard (1909) from the material of the Sichel Herbarium, identified and labelled by Giraud and which is deposited at the MNHN in Paris. Houard (1909) transcribed the original Giraud’s labels and, on the basis of gall drawings in Darboux & Houard (1907), considered *C. catilla* as an intraspecific variation of *Andricus stefanii* (Kieffer, 1900). No other records of the gall are known, and the adults have been remained undescribed.

We tried to find Kieffer’s types of *A. stefanii*. It is known that Kieffer usually returned the material he had got from other colleagues and never kept any specimens, what makes difficult or even impossible to find the type series of species described by him. We searched for *A. stefanii* types in several institutions, especially where some Kieffer’s types are deposited, however, do not found them. According to Kieffer’s manner of depositing types, they should be in Stefani’s collection, which unfortunately was destroyed (Horn *et al.* 1990). However, a single specimen of *Andricus stefanii* determined by De Stefani was found in the collection of the Natural History Museum in Vienna (NHMW).

Recently, we found both, adults and galls of *A. catilla*, labelled by Giraud as “*Cynips catilla* m.” in Giraud’s collection in the MNHN (Paris). Although Giraud obviously considered *A. catilla* as a new species, however, he never published it; no references on this species can be find in his papers or in any of his manuscripts, and thus this name is *in litt.*

Materials and Methods

Described adults are coming from Giraud's and Lichtenstein's collections deposited at the MNHN in Paris, while *A. stefanii* comes from NHMW. SEM pictures were taken by P. Ros-Farré, without coating and using low voltage to preserve specimens. Wing and antenna preparations were draw by using camera lucida.

Results

Andricus catilla (Darboux & Houard, 1907)

(Figs 1–3)

Cynips polycera var. nov. ? Darboux & Houard, 1907: 213.

Cynips catilla Darboux & Houard, 1907: 214–215. Gall.

Cynips catilla: Houard 1909: 68–69, 72. Gall.

Type material. Five galls. The lectotype and paralectotypes here designated. The lectotype gall is the upper one from three galls mounted on one pin, labelled with small Giraud's handwriting white label "galle catilla" and. Two paralectotype galls are two other galls on the same pin as the lectotype are deposited at the MNHN in Paris; one paralectotype gall, labelled also as "galle catilla" is deposited in Pujade-Villar collection (University of Barcelona, Spain); two other paralectotype galls, surrounded by plastic, with Giraud's handwriting label "*Cynips catilla* Giraud" also deposited at the MHNH in Paris. The lectotype and 5 paralectotype galls also bear the following additional labels: red Lectotype/Paralectotype and "*Andricus catilla* (Darboux & Houard, 1907), Bellido & Pujade-Villar det. 1999".

Material examined. 64 asexual females and 5 galls were examined: 58 females from Giraud collection, collected from Austria, ex *Quercus* sp.: 10.II: 15 females; 11.II: 14 females; 12.II: 9 females; 14.II: 16 females; without date: 2 females. Two additional asexual females from "type box" of Giraud collection, the first one with a big rectangular white label "20. *Cynips catilla* G. Austria." and another white label "Museum Paris, coll. Giraud"; second female with a white label "Museum Paris. 20. *C. catilla*. Austria. G. Coll. Giraud". Six additional asexual females from Lichtenstein collection, labeled as "*Cynips catilla* Giraud, Museum Paris, Lichtenstein". One pin with 3 galls and a small white label "galle *catilla*", and 2 additional galls surrounded by plastic and labelled as "*Cynips catilla* Giraud". All the material is deposited at the MNHN in Paris, except of 5 asexual females from Giraud collection which are at the University of Barcelona in Pujade-Villar collection.

Description. Asexual female. Length 1.9–3 mm.

Coloration. Mesosoma black, with some dark reddish-brown zones of variable size, mainly between and around notauli; propodeum and scutellar foveae black, in some specimens mesosoma entirely black. Head reddish-brown, black behind ocellar triangle and around clypeal zone. Antennae and legs are brown. Wings hyaline with light pale brown veins.

Head (Fig. 2a) granular-coriaceous, in sparse and short white pubescence, denser around clypeus; 2.3 times as long as broad in dorsal view, and near 1.2 times as broad as high in front view; gena coriaceous, broadened behind eye; POL more or less 2.0. times longer than OOL; OOL 1.5 times longer than diameter of lateral ocellus and equal to LOL; transfacial distance 1.2 times eye height; clypeus conspicuous and rectangular; face with very weak and short radiating striae; diameter of toruli more or less equal to distance between them and slightly shorter than distance between torulus and inner eye margin.

Antenna (Fig. 1b) 14-segmented, 0.67 times body length; pedicel about 1.3 times as long as broad; A3 as long as A2 and 2.5 times as long as pedicel; A5 slightly longer than A6; scape 2.0 times as long as pedicel, shorter than A3; last antennomeres conspicuously longer than broad and A14 2.0 times as long as broad.

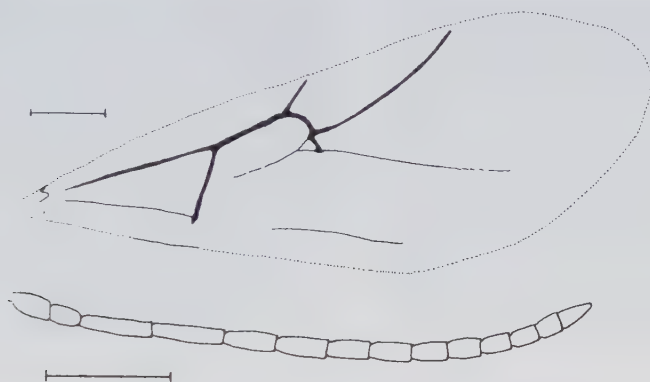


Figure 1 *Andricus catilla*: a, fore wing; b, antenna (scale bar: 0.5 mm)

Mesonotum strongly coriaceous or granular-coriaceous, in sparse white pubescence; notauli complete, deep prolong their length and always reaching pronotum, converging posteriorly (Fig. 2c). Median mesoscutal impression present and conspicuous (Fig. 2c). Mesopleuron and posterior part of lateral surface of pronotum (Fig. 2d) without pubescence, with distinct striae; mesopleuron with some smooth areas. Scutellum rugose, subovate, about as broad as long, not marginate laterally. Scutellar foveae (Fig. 2c) ovate in transverse direction, smooth or alutaceous, without pubescent, each of them well delimited posteriorly by sharp change of sculpture, without any carina, and separated from each other by median carina. Propodeal carinae (Fig. 2b) thin, uniformly thickened, slightly bent outwards, delimiting internal area with some wrinkles and pubescent in upper part.

Wing (Fig. 1a). Fore wing margin ciliate; radial cell 4.0 times as long as broad; distal abscissa of R1 and Rs slightly divergent, not subparallel, 2r curved, areolet big and closed but sometimes only slightly visible because veins blurred.

Legs. Tarsal claws toothed, with small basal lobe; foretibiae with short and oppressed hairs.

Metasoma slightly shorter than head+mesosoma; without pubescence except base of 3rd abdominal tergite; 3rd tergite occupy 0.6 length of metasoma in dorsal view; tergites delicately punctuated; Ventral spine of hypopygium long and slender, around 7.0 times as long as broad, with short and sparse setae, without forming apical tuft.

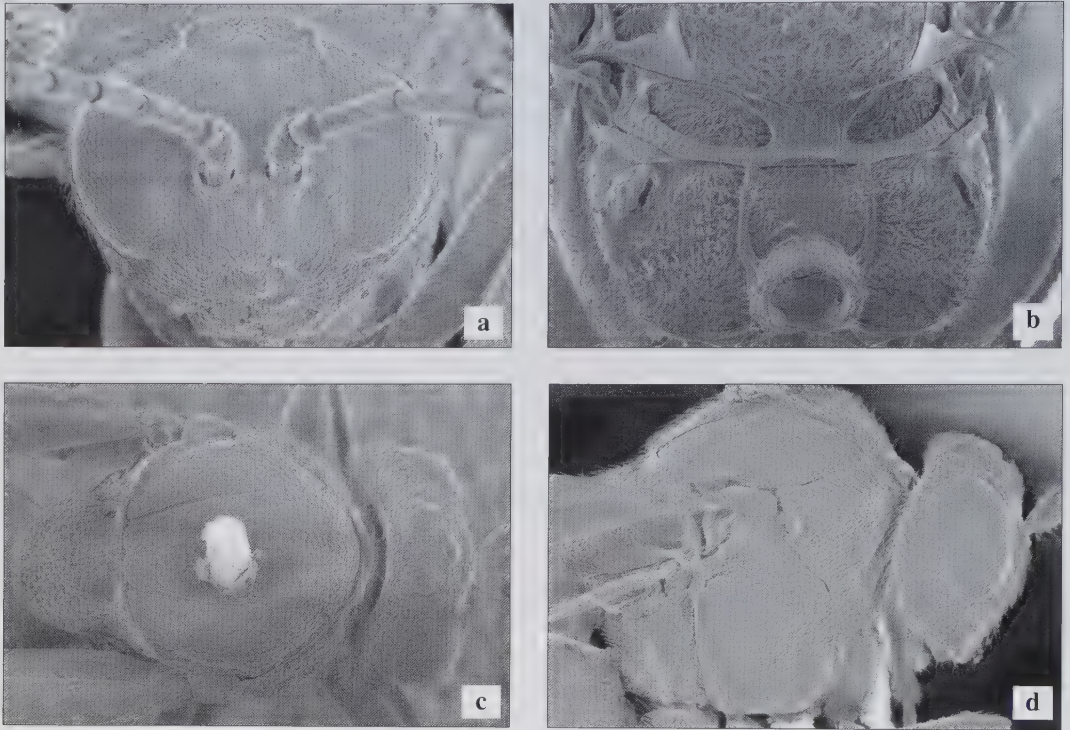


Figure 2 *Andricus catilla*: a, head in anterior view; b, propodeum; c, mesosoma and head in dorsal view; d, mesosoma in lateral view

Sexual form. Unknown.

Gall (Fig. 3) is figured and described in Darboux & Houard (1907) and Houard (1909). Galls are small and very flat (2.3–2.9 mm in total height, and the usual diameter is 7.5–8.5 mm, in some galls only 5.5–6.5 mm. in upper view), with a small larval chamber located at the base of the gall. They are not pedunculated and they have laminar expansions in their upper part. The gall surface is striated laterally and dorsally. According Darboux & Houard (1907) the gall develops from an axillary bud, but unfortunately, neither Darboux & Houard (1907) nor Houard (1909) mentioned the host *Quercus* species, and the labels of the specimens in Giraud's collection do not specify it.

Distribution. Known from Lower Austria only, where Giraud collected the galls. The location of Lichtenstein and Sichel material is unknown.

Andricus stefanii (Kieffer, 1897)

Type material. Neotype female herein designated, with hand-writing white label "Sicil. De Stef. 1899", white label "Collect. G. Mayr", hand-writing white label "C. stefanii Kieff. det. De Stefani", red label "NEOTYPE", white label "Andricus stefanii (Kieffer) Pujad-Villar & Bellido det. 2001"; deposited in NHMW (Vienna, Austria).



Figure 3 Gall of *Andricus catilla* (R=0.7)

According to Horn *et al.* (1990) De Stefani collection was destroyed. No Kieffer's specimens of this species were found in any institution. Probably Kieffer returned the described material to De Stefani and therefore Kieffer's types are lost. Fortunately, in Mayr's collection in the NHMW one single female collected and identified by De Stefani two years after Kieffer's species description was found. Because of possible confusing of *A. stefanii* and *A. catilla*, and also following Art. 75 of the ICZN, we designated herein the neotype of *A. stefanii*.

Discussion

For the first time, *Andricus catilla* as a valid name, with the description of the gall was mentioned by Darboux & Houard (1907). This name also appeared in Giraud's manuscript (Zarazaga, *pers. comm.*). Figures 9 and 10 on plate XIV in Darboux & Houard (1907) are correspond the galls we found in Giraud's collection.

As mentioned above, galls of *A. stefanii* and *A. catilla* are very similar (see also Houard 1909). Nevertheless, *A. catilla* galls differ from *A. stefanii* galls in the absence of a pedicel, which in *A. stefanii* is always present although it can vary from 1.5 to 3.0 mm in length (Kieffer 1897-1901; Houard 1908). They also differ in the surface striation, which is present in *A. catilla* and absent in *A. stefanii* galls. The adults of these species are very different: *A. stefanii* is mainly rusty red coloured, while *A. catilla* with large black areas on the mesosoma and in some specimens the mesoscutum is completely black; scutellar foveae in *A. stefanii* are pubescent, while they are glabrous in *A. catilla*; A3 and A4 are very similar in *A. catilla* while in *A. stefanii* A3 is conspicuously longer than A4. In *A. stefanii* the prominent part of the ventral spine of the hypopygium is rather short, only 3.0 times as long as broad, while in *A. catilla* is long and slender, 7.0 times as long as broad. Finally, fore tibiae in *A. catilla* with short and oppressed hairs, while in *A. stefanii* these hairs are long and erect. So, despite of galls similarity, adults can be easily tell appart.

Melika, Csóka & Pujade-Villar (2000) listed for the Hungarian oak gall cynipid fauna *A. stefanii*, with mentioning *Cynips keszthelyensis* Méhes, 1953 as a nomen nudum and possible synonym of *A. stefanii*. However, authors of this paper never reared adults of this species in Hungary and it was included into the Hungarian fauna list only on the basis of one literature citation

(Ambrus 1974) and collected galls. So, now it is questionable if *A. stefanii* or *A. catilla*, or both species are represented in the Hungarian fauna, due to boarder with Austria, where from *A. catilla* is known. It must be confirmed by further investigations.

Acknowledgements

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ABOUT THE VALIDITY OF *DIPLOLEPIS FRUCTUUM* (RÜBSAAMEN) AND SOME NEW SYNONYMS IN *DIPLOLEPIS NERVOSA* (CURTIS) (HYMENOPTERA: CYNIPIDAE: DIPLOLEPIDINI)

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Abstract – Diagnostic morphological characters for differentiation of *Diplolepis fructuum* (Rübsaamen) from other species of the “*D. rosae* complex” [*D. rosae* (L.), *D. mayri* (Schl.) and *D. spinosissimae* (Gir.)] are given with discussion of characters mentioned by Kierych (1966). A key to species is given; morphological characters for differentiation of *D. fructuum* males are also established for the first time. *Diplolepis andrei*, described by Kieffer from Morocco, is a **syn. nova** to *D. nervosa* (Curtis 1838). Finally, after taking into account recent results in the mitochondrial DNA sequencing and tenuous morphological differences, we consider *D. centifoliae* (Hartig 1840) as a **syn. nova** to *D. nervosa*.

Key words: Hymenoptera, *Diplolepis*, *D. fructuum*, *D. rosae* group, *D. nervosa*, synonymy

Introduction

Diplolepis fructuum (Rübsaamen 1895) (Cynipidae: Cynipinae, Diplolepidini) belongs to the “*rosae*” complex (*sensu* Plantard *et al.* 1998). This group includes 4 species (*D. rosae*, *D. mayri*, *D. fructuum* and *D. spinosissimae*) with a natural Palaearctic distribution (Fig. 1). Morphologically, the “*rosae*” complex is characterised (Pujade-Villar 1993) by having a more or less ovate head; the first antennal flagellomere is 1.7 times as long as the second, straight in females and weakly curved and incised in males; the posterior medial impression of the mesoscutum is usually absent and the scutellum is posteriorly rounded. Galls which it induce are included into the plant tissues of different *Rosa* species and it is impossible to separate them from the plant tissues.

In the original description of *Diplolepis fructuum* (Rübsaamen 1895), the specific status of the insect populations producing galls on *Rosa* fruits in Crimea was already questioned by Rübsaamen (1895). Later, Dalla Torre and Kieffer (1910), followed by Belizin (1957), Kierych (1966) and Zerova & Diakonchuk (1976), who studied this group of species, considered *D. fructuum* as a southern race and thus a synonym of *D. mayri* (according to Russian authors) or as a valid species (according to Kierych, 1966). Posteriorly, Pujade-Villar (1993) could not include *D. fructuum* in his revision but Plantard *et al.* (1998), after their molecular study, affirmed that this was a valid species. For all these reasons, morphological studies on *D. fructuum* are carried out in this paper to differentiate it from other species of the “*rosae*” complex.

Materials and Methods

The type material of *Diplolepis fructuum* has been examined (Pujade-Villar 1993). More than one hundred specimens of *D. mayri* and *D. rosae* and some *D. spinosissimae* from the Iberian Peninsula, Andorra and France were examined together with some material obtained from Iran, Turkey and North Africa.

Figures published in earlier studies (Kierych 1966; Pujade-Villar 1993) we referenciate here as K and P-V, respectively.

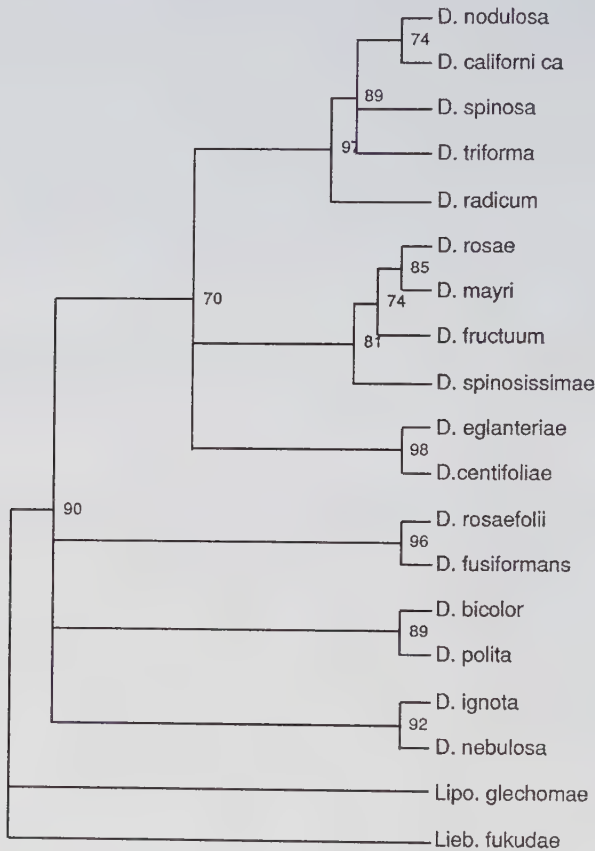


Figure 1 Tree based on 1000 puzzling steps using the combined 12S and Cytochrome b data (according Plantard *et al.* 1998). The *rosae* complex branch has been highlighted in bold

We follow the current terminology of morphological structures as given in Gibson (1985); Ronquist & Nordlander (1989), and Fergusson (1995). Abbreviations for forewing venation follow Ronquist & Nordlander (1989). The measurements and abbreviations used here are: A1 to A15, 1st and subsequent antennomeres; POD (post-ocellar distance), the distance between the inner margins of the posterior ocelli.

Below we discuss only specific characters of each species and giving a key to species identification. Species descriptions are not included because of limited space and they already published and can be find in the original species descriptions and above-mentioned papers.

Results and Discussion

Diplolepis fructuum (Rübsaamen, 1895)

Type material: *Rhodites fructuum* Rübsaamen – 4 light microscope preparations, deposited in Zoologisches Museum (Berlin, Germany).

Material examined: 1 female & 5 males Teleghan (Iran), galls collected by Dr. Hossein Goldansaze in winter 1994-95. 4 males reared from galls collected by Dr. Graham Stone in Turkey in 1997.

Historical review

Rübsaamen (1895) proposed *Rhodites fructuum* as a possible name for a few specimens reared from galls collected from *Rosa canina* deformed fruits in Crimea. He did not describe it as a separate, distinct, because onto his opinion they were closely related to *D. rosae*.

Dalla Torre & Kieffer (1910) on the basis of Rübsaamen's description only, without type examination, considered *D. fructuum* as a dubious species.

Kuznetsov-Ugamskij (1928) differentiated two morphologic types of *D. mayri* galls collected in Turkmenistan. The first one causes hypertrophy and deformation of developing rose fruits and, onto our opinion represents *D. fructuum* galls, while the second type is represented by much smaller sized and more numerous galls forming later on different vegetative parts of the plant. Unfortunately, this author do not reared the wasps from the two gall types.

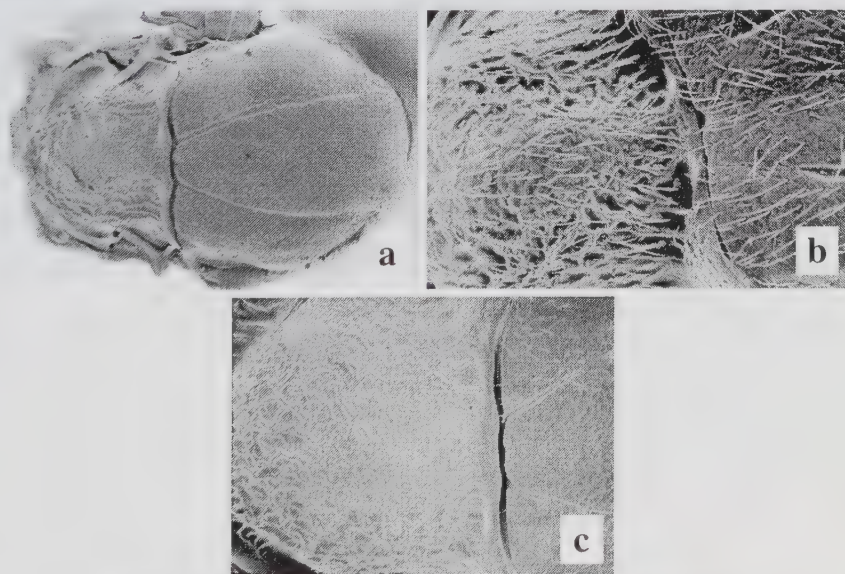


Figure 2 Mesoscutum and scutellum area in dorsal view:
a, *Diplolepis mayri*; b, *D. fructuum* c, *D. rosae*

Belizin (1957) assumed that *D. fructuum* is a geographical race of *D. mayri* and named it as *D. mayri* race *fructuum*. Kierych (1966), after studying a lot of material from Crimea and Caucasus, concluded that *D. fructuum* is a valid species and he indicated the morphological differences between the females of this species and those of *D. rosae* and *D. mayri*. Later, Zerova & Diakontshuk (1976) accepted Belizin's opinion on this species and *D. fructuum* was again controversial.

Pujade-Villar (1993) do not included *D. fructuum* in his European revision even after studying the type material, which is represented by light microscope slide preparations, due to the fact that it was impossible to study the structural characters mentioned by Kierych (1966) and because although some galls collected from Eastern Europe and which possibly belong *D. fructuum* gave no adults for studies.

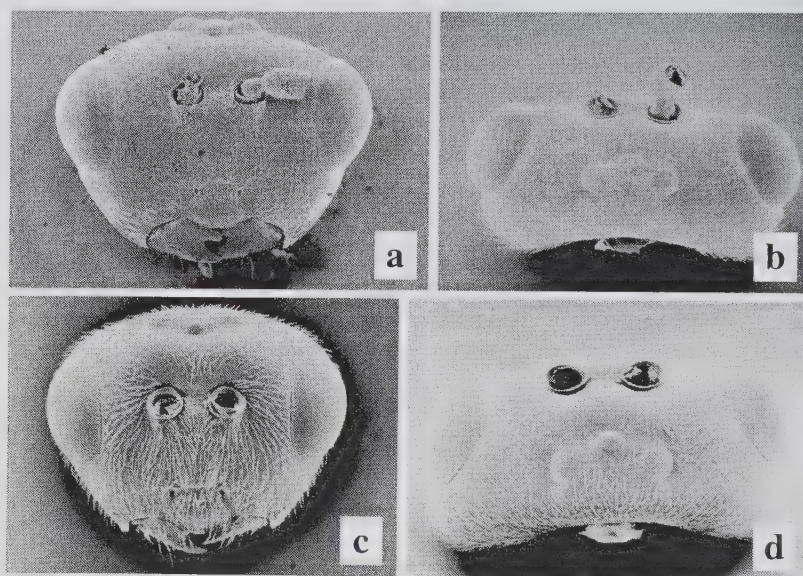


Figure 3 Head in frontal view (a, c) and in dorsal view (b, d):
a, *D. mayri*; b, *D. rosae*; c, d, *D. fructuum*

Molecular studies (Plantard *et al.* 1998) suggested that *D. mayri*, *D. rosae* and *D. fructuum* are three valid species (Fig. 1); the number of substitutions (32 out of 386 bp of a partial sequence of the Cytochrome B gene) between *D. mayri* and *D. fructuum* is similar to other interspecific comparisons.

Discussion

Considering the recently obtained molecular data (Plantard *et al.* 1998) and taken into account two different opinions: *D. fructuum* is a valid species (Kierych 1966) or just a southern race of *D. mayri* (Belizin 1957), further we try to find morphological and other kind of evidences

for separation this species from the “*rosae*” species complex: *D. mayri*, *D. rosae* and *D. spinosissimae*.

Diplolepis fructuum ‘versus’ *D. mayri*

Gall differences. Galls of *D. fructuum* are similar to *D. mayri* only in their external morphology, especially when the galls of the last species develop on *Rosa* spp. fruits. Nevertheless, *D. fructuum* galls are produced by the hypertrophy of seeds inside the fruit, whose development can finally split the external envelope of the fruit. In this case, each seed is modified into an egg-shaped multilocular gall, containing up to ten larval cells and reach a size of 15 x 12 mm; one fruit can include 20 seeds and its can be modified into a large multilocular gall (see Figs 12 or 13 in Kierych (1966) or Figs 4 to 7 in Kuznetzov-Ugamskij (1928)). Galls of *D. mayri* do not split the external envelope of the fruit.

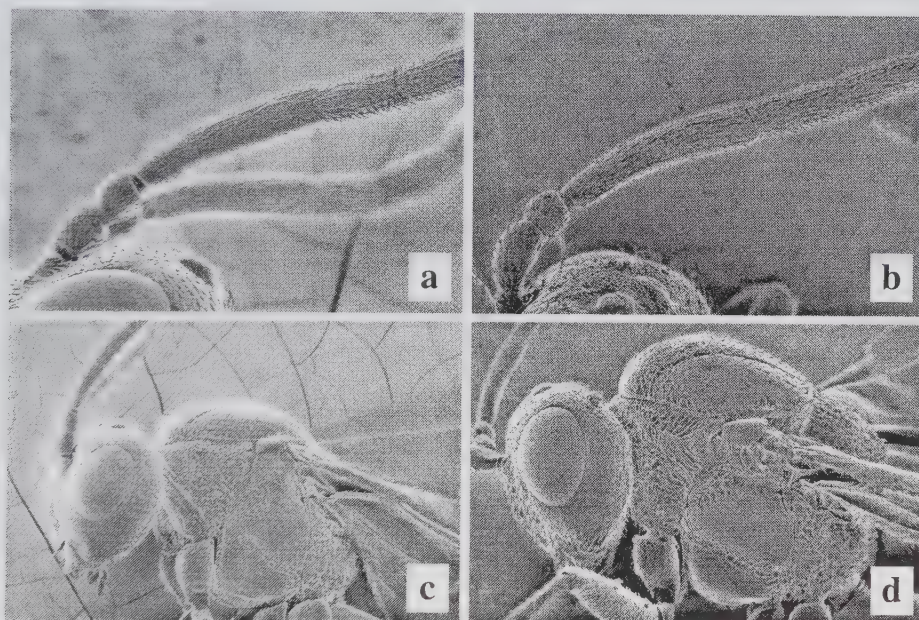


Figure 4 First antennal flagellomeres (a, b) and head plus thorax in lateral view (c, d): a, c, *D. fructuum*; b, d, *D. rosae*

Morphology of adults. Morphologically adult females of *D. fructuum* and *D. mayri* are very similar. Nevertheless, according to our observations, *D. fructuum* differs from *D. mayri* in the shape of the head, structure of the scutellum and forewing. *Diplolepis mayri* and *D. rosae* have a trapezoidal-shaped head (Fig. 3a) in frontal view, while in *D. fructuum* it is more ovate (Fig. 3c). In *D. mayri* the septum between scutellar foveae is broad and coriaceous, the middle of scutellum is also coriaceous (Fig. 2a; Figs K2, P-V4), whereas in *D. fructuum* the septum is narrow (sometimes with a single and long carina), the scutellum is entirely rugose (Fig. 2b; Fig. K3); both characters are more conspicuous in females than in males. The scutellum in *D. mayri* is always

rounded (Fig. 2a; Fig. K2) and normally more or less pointed in *D. fructuum* (Fig. K3). The 2r vein in the radial cell of fore wing of females with a short projection in *D. fructuum* (Fig. K7) but with a longer projection in *D. mayri* (Fig. K6 & Fig. P-V13); in males this projection is short in *D. mayri* and inconspicuous in *D. fructuum*. The areola of forewing, mentioned by Kierych (1966) is present only in some females of *D. fructuum*; the males of this species have a small areola as in males and females of *D. mayri*. The characters of propodeum, mentioned by Kierych (Figs K9, K11) are variable; in *D. fructuum* sometimes a median longitudinal carina can be present (Fig. K11). The shape of male antennae is similar in both species (see Fig. 4a for *D. fructuum*). The lateral surface of pronotum of *D. mayri* in the superior part with a strong transverse carina and the entire pronotum is rugose (as in Fig. 4d), while in *D. fructuum* this carina is very weak and the pronotum is smooth medially (Fig. 4c).

Diplolepis fructuum 'versus' *D. rosae*

Females of *D. rosae* and *D. fructuum* are also differs in the morphology of the head (see above), scutellum and forewings. The septum between scutellar foveae in *D. fructuum* (Fig. 2b; Fig. K3) is narrow (sometimes with a single and long carina); while the scutellar foveae in *D. rosae* are weakly defined (Fig. 2c; Fig. P-V3), and although the interseptum is broad (as in *D. mayri*), it is difficult to establish where its lateral margins are; and, thus, the interseptum looks smaller than it is. The areola in females forewing is large in *D. fructuum* (Fig. K7), and smaller in *D. rosae* (Figs K5, P-V14). The morphological characters of scutellum and forewing of males of both species are much more similar. Nevertheless, A2 in the male antenna is longer than broad and A3 less curved in *D. fructuum* (fig 4a) than in *D. rosae* (Fig. 4b); radial cell 2.0-2.1 times as long as broad in *D. rosae*, while 2.6 times as long as broad in *D. fructuum*. Notauli are incomplete in males of *D. rosae*, while complete in males of *D. fructuum*; while females of both species have an incomplete notauli. Finally, the scutellum is always rounded in *D. rosae* (Figs K3, P-V3) and normally more or less pointed in females of *D. fructuum* (Fig. K3).

Diplolepis fructuum 'versus' *D. spinosissimae*

Diplolepis fructuum is also morphologically closely related to *D. spinosissimae*: in both species, the females have a rectangular head in dorsal view and the males have a longitudinal medial carina on the scutellum. Nevertheless, the chromatic characters are differ: metasoma black in *D. spinosissimae*, and with reddish areas in *D. fructuum*; notauli are much stronger converged posteriorly in *D. spinosissimae* (Fig. P-V2); forewings uniformly darkened in *D. spinosissimae*, without additional vein in 2r (Fig. P-V15). The POD:OOD ratio is variable in females of *D. fructuum* and usually POD is equal OOD, while in *D. spinosissimae* (Fig. P-V19); *D. mayri* and *D. rosae* females OOD is always longer than POD (Fig. 3b; Fig. P-V20).

Conclusions

Diplolepis fructuum is morphologically a valid species. It can be differentiated from other species of *rosae* complex by the following key (partially from Pujade-Villar (1993)):

- 4- Notauli complete and strongly converge posteriorly (Fig. P-V2); medial mesoscutal impression present in 1/3 posterior part of scutum; forewing uniformly dark; 2r angled, without medial additional prolongation; metasoma black; induce spherical and unilocular galls on leaves and petiole *D. spinosissimae* (Giraud)
- Notauli complete or not, never strongly converge posteriorly (Fig. 2a; Fig. P-V3); medial mesoscutal impression absent or inconspicuous (Fig. 2; Fig. P-V3-4); female forewing darkened, more intensely near radial cell; 2r with or without medial additional prolongation; metasoma partially reddish; galls usually in coalescent mass, rarely in leaves and petiole; their surface with filamentous branched hairs or with surface sparsely covered with short unbranched spine. 5
- 5- Interspace between scutellar foveae and entire scutellum (Fig. 2c) rugose; interspaces between the carinae are coriaceous; 2r in female angled, with very short additional vein or without it; A2 in male as long as broad or shorter than broad (Fig. 4b); A3 slightly curved (Fig. 4b); galls usually located on twigs, sometimes in leaves; surface closely covered with very long branched tangled red hairs *D. rosae* (Linnaeus)
- Interspace between scutellar foveae and disc of scutellum coriaceous (Fig. 2a, b); 2r in female with medial additional prolongation into radial cell; A2 in male longer than broad (Fig. 4a); A3 straight (Fig. 4a); galls located on twigs or in fruits; surface sparsely covered with short unbranched spines 6
- 6- Septum between scutellar foveae narrow, with longitudinal projection in centre of scutellum (Fig. 2b); scutellum usually pointed distally in both sexes, more conspicuously in female; pronotum dorso-laterally with large smooth area in male (Fig. 4c); 2r in male with short projection or without it; fused galls in fruits, with a split of cynorhodon – external envelope of the fruit *D. fructuum* (Rübsaamen)
- Septum between scutellar foveae narrow and flat (Fig. 2a); scutellum rounded distally; pronotum rugose dorso-laterally (Fig. 2d); 2r in male with projection into radial cell; coalescent galls, usually on twigs, rarely in fruits but in this case they do not split the external envelope of the fruit *D. mayri* (Schlechtendal)

Diplolepis nervosa (Curtis, 1838) and *Diplolepis centifoliae* (Hartig, 1840)

Diplolepis nervosa (Curtis, 1838).

Cynips nervosa Curtis, 1838.

Rhodites centifoliae Hartig, 1840, syn. nova.

Rhodites rosarum Giraud, 1859 [synonym in Pujade-Villar 1993].

Rhodites andrei Kieffer, 1904, syn. nova.

Rhodites kiefferi Loisele, 1912 [synonym in Pujade-Villar 1993].

Rhodites dispar Niblett, 1943 [synonym in Eady & Quinlan 1963].

Pujade-Villar (1993) suspected that *D. centifoliae* and *D. nervosa* are synonyms because the earlier given diagnostic chromatic differences and the shape of the radial cell could be simply intraspecific variabilities. Moreover, both species have in common a false posterior medial furrow on the scutum, which is visible in the electronic stereo microscope as the result of disorganisation of the central sculpture (Fig. P-V5-6). Sequences of the mitochondrial gene Cytochrome b of this two species reveal very few substitutions (7 out of 386 bp), hence suggesting intraspecific rather

than interspecific variation (Plantard *et al.* 1998). Thus, we consider *D. centifoiliae* as a synonym of *D. nervosa*.

Kieffer (1904) described a new species from Tanger (Morocco), *D. andrei*. Three males from the original series are lost. The gall of this species is unknown (Kieffer 1904). After consulting the original description and after considering *D. centifoiliae* as a synonym of *D. nervosa*, the characters mentioned by Kieffer (1906): the sculpture of the scutum and scutellum and the relative length of A3 and A4, suggest that *D. andrei* is also a new synonym of *D. nervosa*.

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THE LOSS, MODIFICATION AND DEVELOPMENT OF CHARACTERS DURING THE EVOLUTION OF THE EULOPHIDAE (HYMENOPTERA: CHALCIDOIDEA)

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Abstract – Based on world material, the morphology of the Eulophidae has been studied for the first time. Certain morphological characters confirm their ecological adaptations, lifeway and associations with their hosts. Developments of head and metasoma appendages are frequent because they are very important structure in the evolution of parasitism by eulophids. Moreover, many morphological characters could have taxonomic significance.

Key words: Hymenoptera, Eulophidae, morphology, modification, evolution, ecological adaptation

Introduction

Numerous morphological characters have been analyzed among species and genera within the Eulophidae (Bouček 1988; Hansson 1996; Gibson 1997; Yefremova 1995, 1997, 1997, 2001). Although the morphological variations within described species are limited the most reliable morphological distinction between species could be beneficial for taxonomy. The investigators who touched the morphology of eulophids, usually have given only taxonomical aspects. Comparative morphology of eulophids has not been studied. Some morphological characters, such as reduction of structures, fusion and morphological development could be useful for establishing evolutionary scenarios and finding out evolutionary direction of transformation of the head and metasoma appendages. Most of the basic trends of morphology are connected with evolution of the parasitism of the Eulophidae.

Materials and Methods

The material of Eulophidae used in this study was obtained by using a sweep-net when on fieldwork or by the author and her colleagues by rearing from the species' hosts. The specimens were mounted soon after capture or placed in paper envelopes laid in cotton wool. I use the method of slide mounting in balsam as described by Noyes (1982). The specimens examined ($n = 350$) have been drawn. Besides my own specimens, I have investigated material in ZIN (Zoological Institution of Russian Academy of Science, St. Petersburg), BMNH (The Natural History Museum, London), TMLF (Tiroler Landesmuseum Ferdinandum, Innsbruck). For morphological research I have prepared more than 500 figures by light microscopy and 25 illustrations using scanning electron microscopy.

Results

The following evolutionary modifications have been found in the Eulophidae.

Head and its appendages. It has been discovered that the appearance of the frontal fork (composed of the X-shaped frontal grooves that are connected to the ventral scrobes) of the face in the subfamilies Entedoninae and Euderinae is associated with endoparasitism. Species of the subfamily Eulophinae, which are ectoparasitic, never have a frontal fork.

Tentorium. The tentorium of eulophids varies in structure and in its anterior, dorsal and posterior arms. The dorsal arms of some eulophids are lost or have moved position to the toruli (Fig. 1). The anterior tentorial arms are well developed and terminate in the anterolateral part of the clypeus, which is known as the tentorial pits (many eulophids lack tentorial pits except *Hoplocrepis* sp., *Semielacher* sp., *Aulogymnus aceris* Foerster, or are sometimes visible only in the male (*Chrysocharis alpinis* sp. nov. Yefremova 2001). The tentorial pits are situated in the epistomal sulcus of the head capsule. The posterior tentorial arms look like broad tubes. The lower bridge in eulophids looks like a broad sclerotized plate. The upper tentorial bridge has two modifications, viz. it comprises two or four parts (*Miotropis*) (Fig. 2). Dzhanokmen (1995) has commented on the interruption of the upper bridge in the Pteromalidae, but she did not record how many prominences there are in this group.

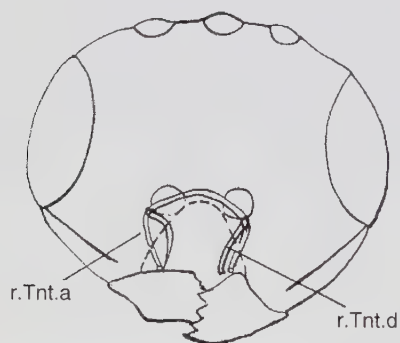


Figure 1 Anterior and dorsal tentorial arms of *Elachertus olivaceus* Thomson, female (dorsal view) ($\times 120$) (r.Tnt.a – anterior tentorial arm; r.Tnt.d – dorsal tentorial arm)

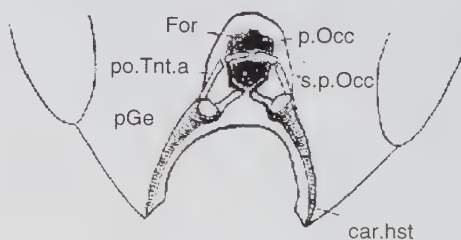


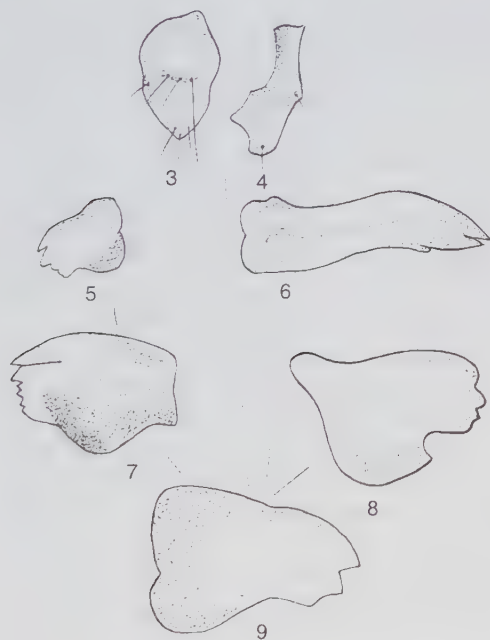
Figure 2 Part of structure of tentorium of *Miotropis unipuncta* Nees, female ($\times 630$) (For – foramen; p.Occ – post-occiput; po.Tnt.a – upper tentorial bridge; s.p.Occ – postoccipital suture; pGe – postgena)

The labio-maxillary complex is attached to the tentorial pits of the head capsule. I have discovered some modifications in the labio-maxillary complex, viz. a decrease in the number of elements of the labial and maxillary palpi: from 2+4 to 1+2 and to 1+1 (*Pediobius* sp.). The Eulophidae have only one paraglossa (not paired, as in many Hymenoptera); moreover, the paraglossa is sometimes partly reduced or lacking.

The primitive chalcid mandible has three teeth. The Eulophidae have developed in a different direction during its evolution: 1) a decrease in the number of teeth; 2) an increase in the number of

teeth; 3) modification (new shape) of the mandible (*Dasyeulophus gelechia* Schauff & LaSalle, *Paraolinx lineatifrons* Ashmead, *Grotiusomyia nigricans* Howard); 4) partly, namely rudimentary (*Cobarus planus* Boucek, *Eulophus* sp., *Hoplocrepis* sp.) or a fully reduced mandible (*Euplectrus*, *Aroplectrus*, *Platyplectrus*) (Figs 3-9). Some entedonine species have a 2-toothed teeth mandible (*Pediobius* sp., *Kokandia salsolicola* Yefremova).

Antenna. The common direction of evolutionary transformation of the antennae is oligomerization, because the antenna has the most numerous equivalent structures such as the segments of the flagellum. Females and males have had different transformations of their antennae. The female antennae are used for the host larva search and, thus have only one function, it is therefore more conservative. More modifications are found in the antennae of the male, as their function involves finding females for copulation. That is why the male antennae have more trichoid and placoid sensillae; the presence of dorsal protuberances or branches on the antenna; developments such as a swollen scape in which there are pores; presence of whorled setae on the funicle; a decrease in the number of anellii and the number of club segments. Two later modifications are also characteristic of the female (Fig. 10).



Figures 3-9 Main evolutionary transformations of mandible in the Eulophidae. 3, *Eulophus pennicornis* Nees; 4, *Eulophus larvarum* L.; 5, *Diglyphus crassineurus* Erdős; 6, *Cocandia salsolicola* Yefremova; 7, *Parasecodes longigaster* Yefremova & Shroll; 8, *Tetrastichus trjapitzini* Kostjukov; 9, *Pnigalio tridentatus* Thomson

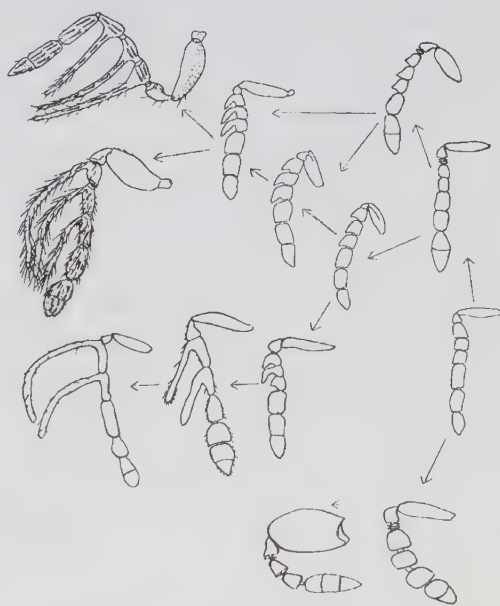


Figure 10 Evolutionary transformation of male antennae during the evolution of the Eulophidae

I will not mention in detail the modification of the mesosoma and its appendages (wing and leg). Reduction of the veins of the forewing characterises all subfamilies of Eulophidae (except the Euderinae). I have never seen full reduction of veins in the Eulophidae (except in the genus *Xanthellum* in which the females have rudimentary wings). Some legs of eulophids have lost one segment in the trochanter, but on the other hand many species of eulophids have an additional long hind spur.

More important modifications are found in the male genitalia and the female ovipositor.

Structure of male genitalia: phallobase, aedeagus, parameral plate, volsellar plate, digitus.

The aedeagus has several modifications:

- divided into two parts (*Dahlbominus fuscipennis* (Zetterstedt), *Chrysocharis* sp., *Elachertus* sp., *Euplectrus bicolor* Swederus, *Miotropis* spp., *Di cladocerus* sp.);
- divided only in the distal part (*Aulogymnus gallarum* L., *Diglyphus* sp., *Pnigalio* sp., *Sympiesis albiventris* Storozheva, *Sympiesis abureana* Waterston)
- completely fused (*Eulophus smerinthica* Bouček, *Euderus* sp., *Zagrammosoma variegatus* Masi, *Aprostocetus* sp.)

The ratio of the length of the aedeagus varies considerably from 2 times (*Ratzeburgiola* sp., *Aprostocetus dubius* Waterston, *Eulophus ramicornis* Fabricius; 2.5 times (*Aulogymnus gallarum* L., *Diglyphus* sp., *Cirrospilus* sp., *Zagrammosoma* sp., *Dahlbominus* sp.; 3 times (*Sympiesis abureana* Waterston).

The parameral plate can also be modified. Some parameral plates are short and very broad and are never separated from the phallobase; they have one seta (*Zagrammosoma* sp., *Sympiesis abureana* Waterston, *Ratzeburgiola incompleta* Bouček, *Elachertus kopetdagensis* Yefremova, *Eulophus larvarum* L., *Chrysocharis* sp.), other species have two setae: *Eulophus smerinthica* Bouček, *Dahlbominus* sp., *Diglyphus isae* Walker, *Perditorulus* sp., *Sympiesis abureana* Waterston), and at last some species have lost the setae, e.g. *Cocandia salsolicola* Yefremova.

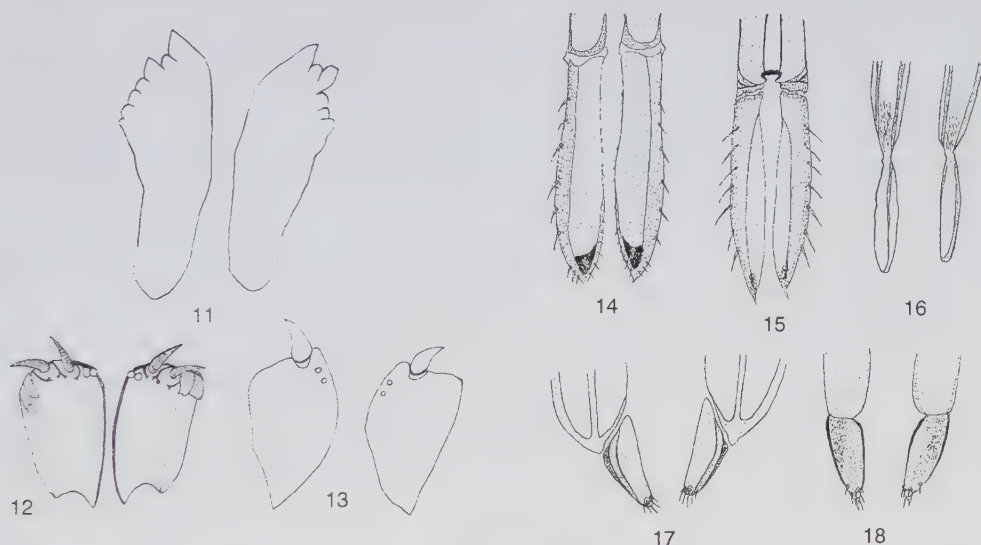
In other species the parameral plates are long and very narrow, are separated from the phallobase and have two setae (Tetrastichinae). The digitus has many various modifications: shape, position in relation to the phallobase, number of spines.

Most eulophids have the digitus parallel to the phallobase (except *Euderus* sp., subfamily Euderinae and some species of Entedoninae, *Perditorulus* (Hansson 1996)). The shape could be like that of a bread glove or triangular. The number of digital spines varies. I have discovered a digitus without spines; this digitus has finger-like appendages Fig. 10). In others, the digitus can have spines numbering from 6-7 (*Eulophus* sp.), 4 spines (*Ratzeburgiola* sp.) 2 spines (*Diglyphus* sp., *Diaulinopsis* sp., *Dahlbominus* sp., *Cocandia salsolicola* Yefremova) to 1 spine (*Aprostocetus dubius* Waterston). If one finds only one spine, it means that there are also several reduced spines. The presence of many spines is a plesiomorphic state (Figs 11-13).

The volsellar plate is, as a rule, reduced in most Eulophinae, but I discovered volsellar plates (*Euderus palustris* Erdős, *Zagrammasoma variegatus* Masi, *Sympiesis albiventris* Storozheva, *Chrysocharis alpinus* Yefremova sp. nov. (in press) and *Elachertus* sp.). Hansson (1996) also mentioned the presence of volsellar plates in the Entedoninae.

Structure of ovipositor: Gonopophyses VIII comprise a long sharp sclerite with arms at the base. The distal parts of the gonopophyses have numerous teeth (*Eulophus* sp., one species of *Zagrammosoma*; these species have a lance-shaped gonopophyses without teeth); gonopophyses

IX is also a long sclerite. The distal part of this structure has a lot of median and lateral teeth, more than in gonopophyses VIII. Moreover, the arms of this gonopophyses have coeloconic sensillae that have been discovered in the following genera: *Ratzeburgiola* sp., *Cirrospilus* sp., *Elachertus* sp., *Miotropis* sp., *Aulogymnus* sp., *Eulophus* sp. (Yefremova 1996). Both gonopophyses have bulbous gonopophysales that contain furcula and musculature to which ligaments are connected. The furcula is a V-shaped sclerite and has a foramen (*Ratzeburgiola* sp., *Cirrospilus* sp., *Aulogymnus* sp., *Grotiusomyia nigricans* Howard); other genera have separate furcula (*Euplectrus* sp., *Dahlbominus* sp., *Chrysocharis* sp., *Pediobius* sp.).



Figures 11–13 Modifications of digitus of male genitalia. 11, *Elachertus kopetdagensis* Yefremova; 12, *Ratzeburgiola incompleta* Bouček; 13, *Aprostocetus dubius* Waterston

Figures 14–18 Variation of gonostyle XI ($\times 630$). 14, *Ratzeburgiola incompleta* Bouček; 15, *Cirrospilus pictus* Nees; 16, *Eulophus larvarum* L.; 17, *Euplectrus bicolor* Swederus; 18, *Platyplectrus babarabicus* Myartseva

Gonocoxite VIII is a small triangular sclerite with a rounded margin. The shape of this sclerite changes very rarely (*Elachertus* with curved sclerite).

Gonocoxite IX is a long sclerite with a protuberant dorso-mesal margin and a strong long latero-ventral part. This sclerite has an apodeme and coeloconic sensillae (4 or 5). Some genera have finely reticulate sculpture in the latero-ventral part (*Aulogymnus* sp., *Eulophus* sp.).

Gonostyle IX or sheath as a rule is sclerotized and has numerous trichoid sensillae except in *Eulophus* sp., *Euplectrus* sp., *Platyplectrus* sp. (Figs 14–18). Some eulophids have coeloconic sensillae on the gonostyle as in *Elachertus* sp. (Yefremova 1998). Ovipositor sheaths IX of some female eulophids exhibit different modifications (Figs 14–18):

- gonostyle IX is articulated with the gonocoxite;
- gonocoxite IX has a sclerotized bridge before joining the gonostyle;

- gonostyle lacks articulation – it is fused;
- gonostyle has a membranous junction with the gonocoxite;
- gonostyle lost its membranous connection and fusion.

Ovipositors are used to puncture hosts that have a dense integument in the smaller species. Morphological research of the eulophid ovipositor has shown that it varies in structure and their junction, depending on its host (Yefremova 1997).

Discussion

Many morphological structures have lost equivalent numbers of modifications during evolution (labial and maxillary palpi, segments of antennae, some structures in the genitalia such as volsellar plates and setae, trichoid sensillae on gonostyle of ovipositor).

Reduction of structures (dorsal tentorial arms of tentorium, mandibular teeth, mandibular glands, reduction of mandible to membranous, reduction veins of forewing to rudimentary wings, spines on digitus of male genitalia).

Fusion of structure (valvae of aedeagus, gonostyle and gonocoxite of ovipositor). Morphological development (unusual shape of mandible and of digitus, appearance of antennal protuberances and branches and third apodeme of ovipositor, which supports gonocoxite IX).

The lost, reduction and fusion of structures have been more frequent than morphological development during the course of evolution. The loss, reduction and fusion in the structure of the appendages of the head, mesosoma and metasoma, the large tagma as in the head, mesosoma and metasoma that were transformed very slowly during evolution. Parasitic wasps of the family Eulophidae have adapted to parasitism by modifying appendages of the body such as antennae, mandibles, wings, legs and the genitalia of both sexes.

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REVIEW OF THE WORLD GENERA OF OAK CYNIPID WASPS (HYMENOPTERA: CYNIPIDAE: CYNIPINI)

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Abstract – The current classification of world genera of Cynipini follows Weld (1952a), who divided Cynipini into 39 genera. Later, Monzen (1954) described a new genus, *Neoneuroterus* from Japan; Maisuradze (1961) reported a new genus, *Reptinia* Belizin & Maisuradze from Ciscaucasus (Azerbaijan); Kovalev (1965) described two new genera, *Belizinella* and *Ussuraspis* from the Far East of Russia; Lyon (1993) synonymized *Xystoteras* to *Phylloteras* and described a new genus, *Euxystoteras*; and Melika & Abrahamson (1997b) described a new genus *Eumayriella* from Florida and synonymized *Trisoleniella* to *Eumayria*. Later, Melika, Ros-Farré & Pujade-Villar (2001) synonymized *Fioriella* to *Plagiotrochus*. Recently 41 genera of Cynipini were known to associate with oaks, generic division of which was based on the presence or absence of a basal lobe on the tarsal claws. A reclassification of world genera of oak gall-inducing cynipids of the tribus Cynipini (Hymenoptera: Cynipidae) is given in which 26 genera are proposed as valid, 15 are synonymized, one *Neuroterus* subgenus, *Latuspina* Monzen, 1954 has an uncertain status; 73 **comb. nov.** and 26 **comb. rev.** are made.

Key words: Cynipidae, Cynipini, gall-wasps, taxonomy

Introduction

The clear definition of genera is the primary difficulty in the classification of Cynipidae (Hymenoptera), particularly in the tribus Cynipini (Dailey & Menke 1980). The presence of alternating asexual and sexual generations in many genera creates considerable morphological variation among adults that markedly complicates the assessment of generic limits and hence classification. The assessment of generic limits requires that generic characters be defined that include the character states of both generations.

Burks (1979) listed 485 species of oak gall-inducing cynipids for North America north of Mexico and subsequent to this publication many new species have been described. Although the majority of North American species of oak gall wasps are known from only one generation, there are nearly 150 species from Central America, mainly Mexico, whose lifecycles are not known. Accumulation of controlled rearing data to determine lifecycles of cynipids will take decades. However, we can improve the classification of the Cynipini by using information from the existing literature on cynipid lifecycles and by detailed analysis of type specimens.

The diagnostic features that are used currently in the keys to the world genera of Cynipini frequently include morphological characters that are inconsistent. Consequently these keys frequently are unable to distinguish some genera. For instance, identification of the representatives of *Plagiotrochus* Mayr, *Bassetia* Ashmead, *Eumayria* Ashmead, *Trisoleniella* Rohwer and Fagan, *Xanthoteras* Ashmead, *Sphaeroteras* Ashmead, and some species groups of *Callirhytis* Foerster are especially complicated. The current systematic arrangement of *Bassetia*, for instance, includes

several *Callirhytis* and *Andricus* Hartig species, *Eumayria* includes some *Callirhytis* species, and *Trisoleniella* appears to be a synonym of *Eumayria* (Melika & Abrahamson 1997b). These systematic difficulties result from the use of inappropriate diagnostic characters for some genera. Such characters are not useful because they are shared by the representatives of several genera and, thus, are inappropriate to use at the generic level. In some cases, the structure and location of a gall or novel host associations were more heavily weighted in the description of new species, species groups, or even new genera than were morphological peculiarities of adult wasps. For example, the North American genus *Heteroecus* Kinsey was established on the basis that its species associate only with *Quercus chrysolepis* Liebm. with distribution limited to California.

A historical review of Cynipidae classification was given in Melika & Abrahamson (2000b). The current classification of world genera of Cynipini follows Weld (1952a). No corrections to Weld's Cynipidae classification were made in a manuscript Weld prepared later entitled "Supplement to Cynipoidea (Hym.) 1905-1950 (1952)." This manuscript, which is dated 1964, is available at the United States National Museum, Smithsonian Institution. Weld's Cynipini classification needs a substantial alteration. It is important to recognize that very little was known about the alternation of generations in North American cynipids during Weld's time. This alone markedly complicated the task of establishing a more natural classification of Cynipini. Excellent studies of the alternation of generations for USA cynipids have been completed during the past several decades (Doutt 1959, 1960; Dailey 1969; Dailey & Sprenger 1973a, 1973b; Dailey, Perry & Sprenger 1974; Evans 1967, 1972; Lyon 1959, 1963, 1964, 1969, 1970; Melika & Buss 2002). These results have increased our understanding of gall-inducing cynipids and given us a better background to establish a more natural classification of Cynipini, particularly for those restricted to North America.

Materials and Methods

Our study analyzed the type species of genera and also many other species types. Specimens were examined from the following museums and institutions: USNM (United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA, A. Menke), AMNH (American Museum of Natural History, NYC, NY, USA, J. Carpenter), CNCI (Canadian National Collection of Insects, Ottawa, Canada, J.T. Huber), BMNH (British Natural History Museum, London, England, J. Noyes, D. Notton and N.D.M. Fergusson), OUM (Hope Entomological Collections, University Museum, Oxford, UK, C. O'Toole and G. McGaven), NHMW (Naturhistorisches Museum, Vienna, Austria, S. Schödl), NHMH (Hungarian Natural History Museum, Budapest, Hungary, L. Zombori and J. Papp), ZIN (Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia, O.V. Kovalev), IZU (Schmalhausen Institute of Zoology of the Ukrainian Academy of Sciences, Kiev, Ukraine, M.D. Zerova and L.V. Diakontshuk), and MNHN (Muséum National d'Histoire Naturelle, Paris, France, C. Villemant-Ait-Lemkadem). In addition, we examined specimens from different genera that were kindly sent to the authors by J. Pujade-Villar (Universitat de Barcelona, Barcelona, Spain), J.L. Nieves Aldrey (Museo Nacional de Ciencias Naturales, Madrid, Spain), G.N. Stone (Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh, Scotland). Authors express their deepest appreciation to mentioned colleagues for help in obtaining material for research. Also the Cynipidae collection of Systematic Parasitoid Laboratory (Köszeg, Hungary) was examined.

We use the following terminology: for mesosoma (Gibson 1985; Menke 1993), for head, metasoma, and ovipositor (Fergusson 1988; Ronquist & Nordlander 1989) (Figs 1-4). The surface sculpturing follows Harris (1979). Abbreviations for the forewing venation follow Ronquist & Nordlander (1989). The measurements and abbreviations used herein include: F1-F12, 1st and subsequent flagellomeres; POD (post-ocellar distance), the distance between the inner margins of the posterior ocelli; OOD (ocellar-ocular distance), the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; LOD, the distance between lateral and frontal ocellus; transfacial line, distance between inner margins of compound eyes measured across antennal sockets (Fig. 1). The width of the radial cell is measured along 2r (Fig. 3). Drawings were made with the aid of a Leica drawing tube or from stereomicroscope photographs, which were scanned into a PC and modified in Adobe Photoshop 6.0.

Results and Discussion

Morphology and current arrangement of genera

The tribus Cynipini (Hymenoptera, Cynipidae) includes species that induce galls on members of Fagaceae, primarily *Quercus* L. with exceptions for only a few species. For instance, *Dryocosmus kuriphilus* (Yasumatsu), the only species of Cynipini known to associate with *Castanea*, threatened the chestnut industry of Japan and Korea and was discovered in Georgia, USA in 1974 (Payne *et al.* 1975). Another species, *Dryocosmus castanopsidis* (Beutenmueller), known from Oregon and California, induces galls on catkins of *Castanopsis chrysophylla* and *C. sempervirens* (Burks 1979).

Three genera, *Liebelia* Kieffer, 1903 *Paraulax* Kieffer, 1904, and *Poncyia* Kieffer, 1903 that were included in Weld's (1952a) Cynipini key belong elsewhere. The genera *Liebelia* and *Diplolepis* Geoffroy, 1762 belong in the Diplolepidini (Ronquist 1999). *Paraulax* possesses some character states (e.g., the structure of the antenna and forewing venation) that indicate the genus should be placed in the Charipinae subfamily (Cynipoidea: Figitidae) (Ronquist 1995). Furthermore, on the basis of its description, *Poncyia* may be a *Plagiotrochus*, or if the description of the pronotum is incorrect, the genus must be placed among inquilines on the basis of its longitudinally striate petiole and long tergum II. Currently it is placed in the Cynipidae, *incertae sedis* (Ronquist 1999). The genus, *Synophrus* Hartig, 1843, with only three known species from Western Palearctic, *S. pilulae* Giraud in Houard, 1911, *S. politus* Hartig, 1843 (Europe, Asia Minor, North Africa), and *S. olivieri* Kieffer, 1899-1901 (Algeria, Israel, Iran), originally was described as a gall inducer, however, on the basis of the morphological characters of adults, this genus belongs to cynipid inquilines (Ronquist 1994). *Synophrus* has never been a subject to detailed research and, thus, it is quite possible, that *Synophrus* species, in spite of their taxonomic identity with cynipid inquilines, lack gall-inducing capability. This genus is also excluded from the below analysis.

Around 1000 species of Cynipini are known worldwide, all in the Holarctic region, mainly in the Western Palearctic (around 140 valid species) and America North of Mexico (Burks (1979) listed 485 species of oak gall-inducing cynipids). The taxonomy of Cynipini species have undergone substantial changes: new names, synonymies, new name combinations, and new alternate life forms were experimentally obtained for several gall wasps. Currently 41 genera of Cynipini are known to associate with oaks (Table 1).

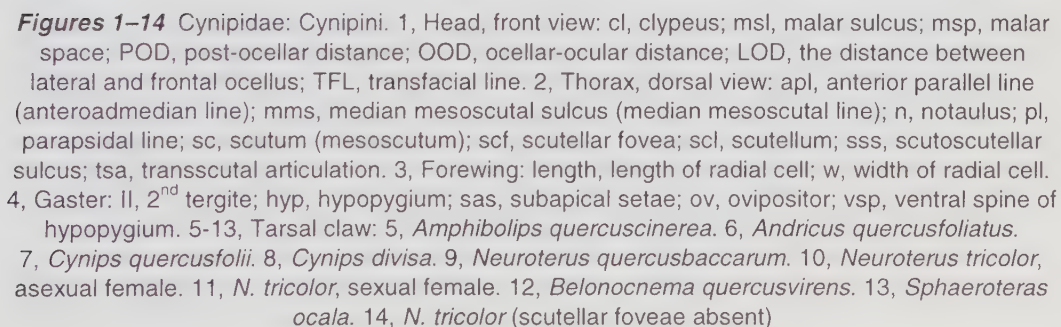
Table 1 Current arrangement of Cynipini genera and their distribution (after Pujade-Villar, Bellido, Segú & Melika 2001, with some changes)

Genus name	Geographic distribution	Number of species
<i>Acraspis</i> Mayr, 1881	Nearctic	probably > 30
<i>Amphibolips</i> Reinhard, 1865	Nearctic	around 30
<i>Andricus</i> Hartig, 1840 (= <i>Adleria</i> Rohwer & Fagan, 1917)	Holarctic and Oriental?	probably > 300
<i>Antron</i> Kinsey, 1930	Nearctic	around 40
<i>Aphelonyx</i> Mayr, 1881	Palearctic	4
<i>Atrusca</i> Kinsey, 1930	Nearctic	uncertain; probably > 40
<i>Bassetia</i> Ashmead, 1887	USA	9
<i>Belizinella</i> Kovalev, 1965	Russia, Far East	2
<i>Belonocnema</i> Mayr, 1881	USA	2
<i>Besbicus</i> Kinsey, 1930	USA	8
<i>Biorhiza</i> Westwood, 1840	Palearctic	2
<i>Callirhytis</i> Foerster, 1869	Holarctic	around 150
<i>Chilaspis</i> Mayr, 1881	Occidental Palearctic	3
<i>Cynips</i> Linnaeus, 1758	Palearctic	around 25
<i>Disholcaspis</i> Dalla Torre & Kieffer, 1910	Nearctic	around 40
<i>Dros</i> Kinsey, 1937	Nearctic	11
<i>Dryocosmus</i> Giraud, 1959	Holarctic	Around 25
<i>Erythres</i> Kinsey, 1937	Mexico	2
<i>Eumayria</i> Ashmead, 1887 (= <i>Trisoleniella</i> Rohwer & Fagan, 1917)	USA	5
<i>Eumayriella</i> Melika & Abrahamson, 1997	USA	2
<i>Euxystoteras</i> Lyon, 1993	USA	1
<i>Heteroecus</i> Kinsey, 1922	USA	15
<i>Holocynips</i> Kieffer, 1910	USA	4
<i>Liodora</i> Foerster, 1869	Europe, USA	3
<i>Loxaulus</i> Mayr, 1881	Nearctic	14
<i>Neoneuroterus</i> Monzen, 1954	Russia, Far East and Japan	5
<i>Neuroterus</i> Hartig, 1840	Holarctic	About 100
<i>Odontocynips</i> Kieffer, 1910	USA	1
<i>Paracraspis</i> Weld, 1952	USA	3
<i>Parandricus</i> Kieffer, 1906	China	1
<i>Philonix</i> Fitch, 1859	USA	8
<i>Phylloteras</i> Ashmead, 1897 (= <i>Xystoteras</i> Ashmead, 1897)	Nearctic	6
<i>Plagiotrochus</i> Mayr, 1881 (= <i>Fioriella</i> Kieffer, 1903)	Western Palearctic & Himalaya	14
<i>Repentinia</i> Belizin & Maisuradze, 1961	Transcaucasus	1
<i>Sphaeroteras</i> Ashmead, 1897	USA	8
<i>Trichagalma</i> Mayr, 1907	Japan and China	2
<i>Trichoteras</i> Ashmead, 1897	USA	8
<i>Trigonaspis</i> Hartig, 1840	Palearctic	Around 10
<i>Ussuraspis</i> Kovalev, 1965	Russia, Far East	1
<i>Xanthoteras</i> Ashmead, 1897	USA	12
<i>Zopheroteras</i> Ashmead, 1897	USA	6

With the exception of the genus *Neuroterus* Hartig, 1840 (Fig. 14) the current classification of the world genera of the Cynipini is based on the presence or absence of a basal lobe (tooth) on tarsal claws (Figs 5-13) (Weld 1952a). The use of this character dates to earlier treatments including Ashmead's (1903) key to 33 genera of Cynipini. Earlier, Mayr (1881), Ashmead (1885), Dalla Torre (1893), Kieffer (1897-1901) used this character for subgeneric level to separate *Callirhytis* and *Andricus* as subgenera of *Andricus*. Again with the exception of *Neuroterus*, Weld (1952a) divided all the genera into two groups: (a) those that possess a basal lobe on tarsal claws and (b), those that have simple tarsal claws without a basal lobe (Table 2). Consequently, the number of oak gall-inducing Cynipini genera distinguished by Weld (1952a) was 39. Later, Monzen (1954) described a new genus, *Neoneuroterus* from Japan; Maisuradze (1961) reported a new genus, *Repentinia* Belizin & Maisuradze from Ciscaucasus (Azerbaijan); Kovalev (1965) described two new genera from Far East of Russia, *Belizinella* and *Ussuraspis*; Lyon (1993) synonymized *Xystoteras* to *Phylloteras* and described a new genus, *Euxystoteras*, which differs from *Phylloteras* only by having simple tarsal claws; and Melika & Abrahamson (1997b) described a new genus *Eumayriella* from Florida and synonymized *Trisoleniella* to *Eumayria*. Later, Melika, Ros-Farré & Pujade-Villar (2001) synonymized *Fioriella* to *Plagiotrochus*. We will discuss these new genera and synonymizations below.

Table 2 Division of the Cynipini based on the presence or absence of a basal lobe on the tarsal claws (* – genera which include species in both groups)

Genera with toothed claw	Genera with simple claw
<i>Acraspis</i>	<i>Aphelonyx</i>
<i>Amphibolips</i>	<i>Bassetia</i>
<i>Andricus</i>	<i>Belizinella</i> *
<i>Antron</i>	<i>Belonocnema</i>
<i>Atrusca</i>	<i>Biorhiza</i>
<i>Belizinella</i> *	<i>Callirhytis</i> *
<i>Besbicus</i>	<i>Chilaspis</i>
<i>Callirhytis</i> *	<i>Dryocosmus</i>
<i>Cynips</i>	<i>Erythres</i>
<i>Disholcaspis</i>	<i>Eumayria</i>
<i>Dros</i>	<i>Eumayriella</i>
<i>Liodora</i>	<i>Euxystoteras</i>
<i>Neoneuroterus</i>	<i>Heteroecus</i>
<i>Paracraspis</i>	<i>Holocynips</i>
<i>Parandricus</i> *	<i>Loxaulus</i>
<i>Philonix</i>	<i>Odontocynips</i>
<i>Phylloteras</i>	<i>Parandricus</i> *
<i>Repentinia</i>	<i>Plagiotrochus</i>
<i>Trichoteras</i>	<i>Sphaeroterus</i>
<i>Trigonaspis</i> *	<i>Trichagalma</i>
<i>Xanthoteras</i>	<i>Trigonaspis</i> *
	<i>Ussuraspis</i>
	<i>Zopheroterus</i>



Thus, classification of the Cynipini has relied on the presence or absence of the tarsal claw (Figs 5-13). Lyon (1993), for example, stated that in cynipid taxonomy "the presence or absence of a tooth on the tarsal claw is considered to be of fundamental importance in separating major genera of the group." However, this morphological criterion, dividing the Cynipini genera into two major groups, is insufficient for all taxonomic distinctions. There are a number of exceptions to this criterion, including those discussed by Weld (1952a). For instance, the majority of *Neuroterus* species have tarsal claws without a basal lobe, however, *quercusbaccarum* L., *numismalis* Olivier, and *petioliventris* Hartig, have toothed tarsal claws with a basal lobe in the asexual generations but simple claws in the alternate sexual generations. The same is true for *Callirhytis*, in which both generations of the European species *glandium* (Giraud) have toothed tarsal claws as the asexual generation of *bella* (Dettmer) (Nieves Aldrey 1992). One species from *Trigonaspis* genus, *T. megaptera* (Panzer) has a weak tooth on claws, while other species, *T. synaspis* have simple tarsal claws. The sexual generations of the North American genus *Xystoteras* have a very weak tooth on claws, and in *Parandricus mairei* Kieffer, the females have toothed tarsal claws while the males have simple claws without a basal lobe. In the genus *Belizinella*, one species, *B. gibbera* Kovalev, has claws with a basal lobe while another species, *B. vicina* Kovalev, have simple claws (Kovalev 1965). The presence or absence of a basal lobe is a likely homoplasy and probably evolved separately in different cynipine genera. The ancestral condition is a simple tarsal claw without a basal lobe, based on its appearance in the majority of genera from the Aylacini. However, even in this tribe, *Xestophanes* Foerster, *Diastrophus* Hartig and *Gonaspis* Ashmead have a basal lobe. An additional complication is the use of the term "tooth" Given that the term basal lobe would be more precise. In some cases the claws have a strong basal lobe, for example as in *Amphibolips* and many *Andricus* species. However in numerous species, including those that Weld treated as possessing a tooth, no distinct tooth occurs on the claws.

This character has been used for generic separation in other Hymenoptera groups as well, as for example in the Chalcidoidea. However, later works reconsidered the diagnostic value of this character in these groups and subsequently dropped it. Anura Wijesekara (Sri Lanka, *pers. comm*) eliminated the use of this character for the separation genera of Chalcididae and Leucospidae; Eric Grissell (*pers. comm.*) attempted to use this character to separate species (but not genera of Torymidae) and found that this character does not work even at the species level.

The main diagnostic characters for genera separation used by Weld (1952a) and characters that we use in genera separation were discussed earlier (Melika & Abrahamson 2000b) and they are provided below.

Acraspis Mayr, 1881

Acraspis Mayr 1881: 2, 29. Type species: *Acraspis pezomachoides* (Osten Sacken, 1862). Designated by Rohwer & Fagan 1917. Types examined. Ashmead 1903 and Beutenmueller 1909 (synonym of *Philonix*). Weld 1922 (*Acraspis* and *Philonix* distinct genera).

Paracraspis Weld 1952b: 324. Type species: *Callirhytis guadaloupensis* Fullaway, 1911. Designated by Weld 1952b. Types examined. **New synonym.**

Diagnosis. Similar to *Philonix*, however, the scutellum of asexual *Acraspis* females is elongated and pointed posteriorly (Figs 25, 26), while in *Philonix* it is rounded (Fig. 27); the projecting part of the ventral spine of the hypopygium in *Acraspis* is equally broad through entire length or slightly tapering to a point at the apex, with dense subapical setae (Fig. 18); in *Philonix*

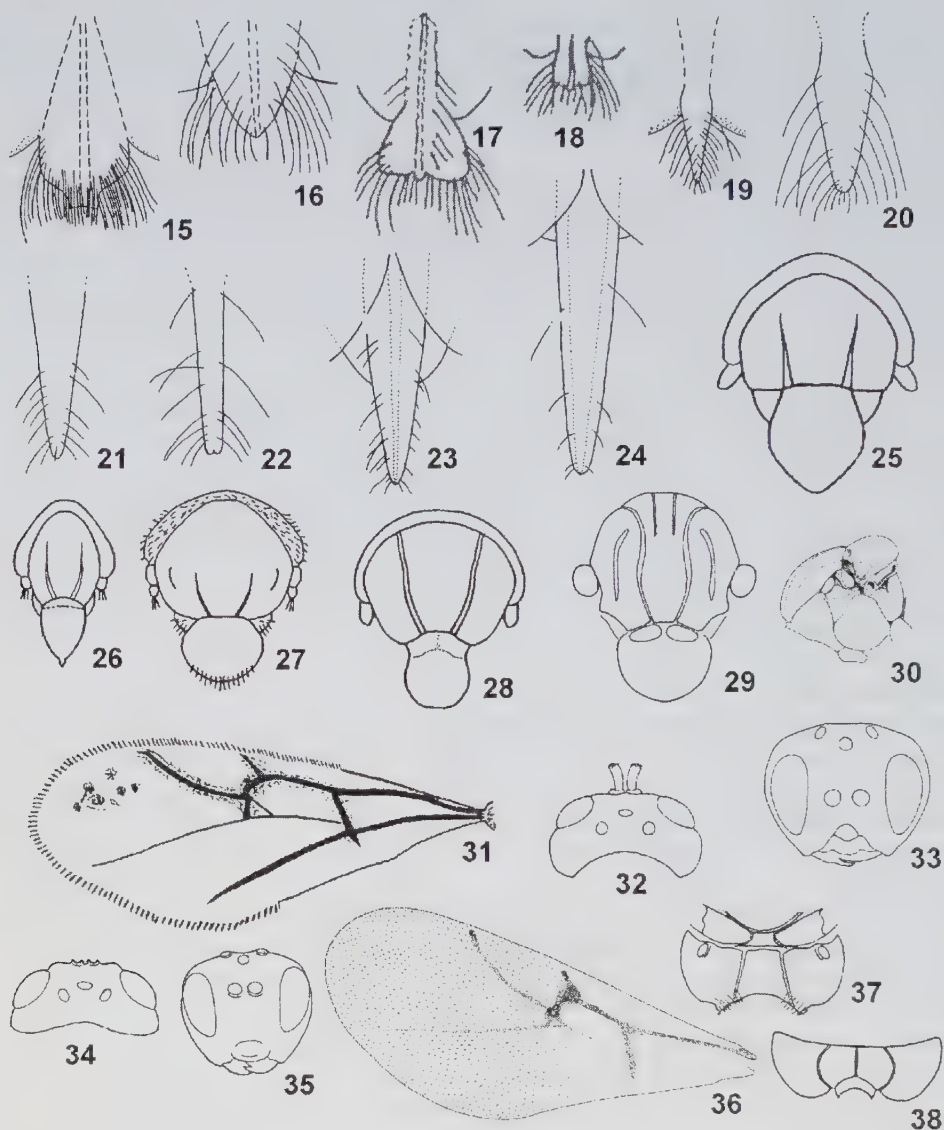
the projecting part of the ventral spine is flattened, broadest at the apex, with long dense subapical setae reaching far beyond the apex of the spine to form a broad truncate tuft (Fig. 17). The asexual females of *Acraspis* also resemble *Biorhiza* but differ in having distally elongated and flattened scutellum, which overhangs the metascutellum and hides the propodeum; the latter declines more strongly than in *Biorhiza*.

In sexual *Acraspis* females, the scutum is coriaceous or microreticulate, bare or with very sparse short setae; notauli are incomplete in the anterior one-third or very indistinct. Closely resembling *Disholcaspis* but F1 of the antenna is equal or very slightly shorter than the scapus+pedicellum; the head is more broad from above; the scutum and mesopleuron are coriaceous, while in *Disholcaspis* F1 is 2.0 times as long as scapus+pedicellum; the head is more narrow from above; the scutum and mesopleuron are more densely reticulate. In *Acraspis* males, F1 is straight or only slightly incised, less than 2.0 times as long as scapus+pedicellum; the scutum is shorter; the scutellum is coriaceous, elongated, gradually and slightly depressed toward the transscutal articulation, without scutellar foveae or transversal groove, with white setae. In *Disholcaspis* males, F1 is 2.0 times as long or longer than scapus+pedicellum; the scutum is longer. We are unable to find appreciable diagnostic characters for the precise separation of *Acraspis* males from *Cynips*. It is, however, possible that *Acraspis* forms a brachypterous species-group within *Cynips* as Kinsey (1930, 1936) proposed. Additional biological experimental data on alternation of generations and/or using of molecular techniques are required to solve this problem. See also Diagnosis to *Cynips*.

Comments. The only diagnostic character given by Weld (1952b) for differentiating his newly described *Paracraspis* from *Acraspis* is that it has “less reduced wings, a more robust thorax with a normally rounded scutellum.” However, the scutellum in *Paracraspis* is longer than broad, slightly overhanging the metascutellum; not tapering posteriorly to a point as in a typical *Acraspis* but distinctly elongated, not rounded as in *Philonix*; the scutum is flattened as in *Acraspis* (Fig. 25). For instance, *A. inflata* (Kinsey) and *A. gemula* var. *suspecta* (Kinsey) have an elongated scutellum, which do not taper posteriorly to a point. Some *Acraspis* species are also densely pubescent. Thus, we consider *Paracraspis* as a **syn. nov.** of *Acraspis*. Three *Paracraspis* species must be transferred to *Acraspis*: *guadaloupensis* (Fullaway, 1911), **comb. nov.**, *insolens* Weld, 1926, **comb. rev.**, and *patelloides* Weld, 1926, **comb. rev.**

Biology. The majority of species are known from the asexual generations only and the galls produced by asexual species are very similar, known commonly as “hedgehog” galls. They are usually globular, hard and slightly elongated, detachable leaf galls, with surface reticulate or rough, with points or spines. The sexual generation induces tiny bud galls. The sexual form was described by Bassett (1881) for the first time as *Cynips gemula*. Triggerson (1914) established alternation of generations experimentally for *A. erinacei* (Beutenmueller, 1909).

Distribution. Seventeen species of *Acraspis* were listed for the United States and Canada (Burks 1979), however, two species must be transferred into *Cynips*: *arida* Kinsey, 1930, **comb. rev.** and *conica* Kinsey, 1930, **comb. rev.** Currently the number of known species is 18. Several species were also described from Mexico (Kinsey 1930, 1936), however, the validity of some species is very dubious and must be revised. Several of them are likely synonyms and several other species described in the *Acraspis* genus must be transferred to other genera.



Figures 15–38 15–24, Ventral spine of hypopygium: 15, *Cynips quercusfolii*, asexual female; 16, *Sphaeroterus ocala*; 17, *Philonix fulvicollis*; 18, *Acraspis echini*; 19, *Cynips longiventris*, sexual female; 20, *Neuroterus laeviusculus*, sexual female; 21, *N. quercusbaccarum*, asexual female; 22, *N. numismalis*, sexual female; 23, *Andricus solitarius*; 24, *A. quercusramuli*. 25–29, Thorax, dorsal view: 25, *Acraspis insolens*; 26, *A. echini*; 27, *Philonix fulvicollis*; 28, *Trigonaspis quercusforticorne*; 29, *Andricus askewi*. 30, *Andricus kollari*, asexual female, mesosoma in lateral view. 31, *Atrusca quercuscentricola*, forewing. 32–33, *Bassetia pallida*, head: 32, from above; 33, front view. 34–35, *Plagiotrochus quercusilicis*, head: 34, from above; 35, front view. 36, *B. pallida*, forewing. 37–38, propodeum: 37, *B. pallida*; 38, *P. quercusilicis*

***Amphibolips* Reinhard, 1865**

Amphibolips Reinhard 1865: 10. Type species: *Cynips spongifica* Osten Sacken, 1862. Designated by Rohwer & Fagan 1917. Types examined.

Trissandricus Kieffer 1910: 115. Type species: *T. maculipennis* Kieffer, 1910. Original designation. Monotypic. Weld 1931 (synonym of *Amphibolips quercusspongifica*).

Diagnosis. The head and mesosoma are dull, coarsely rugose. The mesosoma is robust, highly arched, broader than the head; the scutum is broader than long; the scutellum is subquadrate or cushion-shaped, slightly broader than long, with large, deep and sometimes wrinkled scutellar foveae. The projecting part of the ventral spine of the hypopygium is narrow, needle-like, long, usually more robust and broader than in closely related *Andricus*. The forewing has distinct or less distinct smoky spot(s). Tarsal claws have strong basal lobes. The genus is very uniform in the characteristics of adults and the galls that they induce. The morphology of the asexual and sexual females is identical.

Comments. On the basis of diagnostic characters given above, 6 species from the genus *Andricus* herein are transferred to *Amphibolips*: *A. ellipsoidalis* Weld, 1926, **comb. rev.**, *A. femoratus* Ashmead, 1887, **comb. nov.**, *A. quercusostensackenii* (Bassett, 1863), **comb. nov.** (= *Andricus quercussingularis* (Bassett, 1863), **syn. nov.**), *A. ruginosus* (Bassett, 1890), **comb. nov.**, *A. vernus* Bassett, 1900, **comb. rev.** Galls of these six species structurally are also typical *Amphibolips* galls.

Méhes (1953) described *Amphibolips mernyensis* on the basis of one gall, collected from *Quercus cerris* in Hungary, however it appears to be a nomen nudum (Melika, Csóka & Pujade-Villar 2000).

Biology. Both asexual and sexual generations induce stem, bud and leaf galls, the majority of which are uniform in their structure: the larval chamber occurs in the center of the gall and supported by radiating filaments.

Distribution. North and Central America. With the species transferred herein, 40 species are known: 30 from America north of Mexico (Burks 1979) and 10 from Mexico (Beutenmueller 1911; Kinsey 1937b).

***Andricus* Hartig, 1840**

Andricus Hartig 1840a: 185. Type species: *A. noduli* Hartig, 1840 (= *A. trilineatus* Hartig). Designated by Foerster 1869.

Aphilotrix Foerster 1869: 331, 336. Type species: *Cynips corticis* Linnaeus, 1758. Original designation. Mayr 1881 (synonym of *Andricus*).

Manderstjernia Radoszkowsky 1866: 304. Type species: *M. paradoxa* Radoszkowski. Original designation. Later, the name was determined to be the elder synonym of *Cynips albopunctatus* Schlechtendal.

Oncaspis Dettmer 1925: 123. Type species: *O. filigranata* Dettmer. Original designation. Dettmer 1928 (*O. filigranata* is the sexual generation of *Andricus solitarius* (Fonsc.) and, thus synonym of *Andricus*. Weld 1930 (synonym of *Andricus*).

Euschmitzia Dettmer 1925: 122. Type species: *E. rara* Dettmer. Original designation. Later, the author thought it was the sexual generation of *Andricus nudus* Adler and asked Weld to publish it. Weld 1930 (synonym of *Andricus*).

Femuros Kinsey 1937a: 65. Type species: *F. repandae* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).

Feron Kinsey 1937a: 69. Type species: *F. verutum* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).

- Druon* Kinsey 1937a: 56. Type species: *D. protagion* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).
- Conobius* Kinsey 1938: 262. Type species: *C. strues* Kinsey. Original designation. Weld 1952a (synonym of *Andricus*).
- Adleria* Rohwer and Fagan 1917: 359. Type species: *Cynips kollari* Hartig, 1843. Original designation. Benson in Marsden-Jones 1953 (synonym of *Andricus*).
- Dros* Kinsey 1937a: 49. Type species: *D. petasum* Kinsey. Original designation. Types examined. **New synonym.**
- Erythres* Kinsey 1937b: 461. Type species: *E. hastata* Kinsey. Original designation. Types examined. **New synonym.**
- Liadora* Foerster 1869: 331, 334. Type species: *L. sulcata* Foerster. Original designation. Mayr 1881 (synonym of *Dryophanta*). Dalla Torre 1893 (treated as a separate genus). Dalla Torre & Kieffer 1910 (synonym of their "*Diplolepis* L. Geoffr."). Mayr 1903 (restored its generic status). Types of North American species examined. **New synonym.**
- Parandricus* Kieffer 1906: 102. Type species: *P. mairei* Kieffer. Original designation. Monotypic. Types examined. **New synonym.**
- Trichoteras* Ashmead 1897a: 67. Type species: *T. coquillettii* Ashmead. Original designation. Types examined. **New synonym.**

Diagnosis. Projecting portion of the ventral spine of the hypopygium is needle-like, long, with subapical setae that do not reach beyond the apex of the spine; if short then slender and thin, tapering to point at the apex, at least 2.0 times as long as broad, with short sparse subapical setae which if reaching beyond the apex of the spine then never dense and they do not form a truncate tuft (Figs 23, 24). Mesosoma is arched, notauli usually complete, sometimes absent or indistinct in the anterior 1/3-1/4; scutum is usually as long as broad or subequal, subquadrate; scutellar foveae usually distinct, separated by a median carina (Figs 29, 30).

Comments. Mayr (1881) treated *Callirhytis* as a subgenus of *Andricus*. Dalla Torre & Kieffer (1910) erroneously synonymized *Trisoleniella* Rohwer & Fagan to *Andricus*.

Adleria. Rohwer & Fagan (1917) proposed *Adleria* instead of *Cynips* sensu Authors, which they did not accept along with the type designations. The European species of the former *Cynips* sensu Authors [not *Cynips* Linnaeus!] were transferred to *Andricus* after the sexual generations were discovered and found to have the diagnostic characteristics typical of the sexual *Andricus* (Benson in Marsden-Jones 1953). Zerova, Diakontshuk & Ermolenko (1988), in their review of the gall-inducing insects of the European portion of the former Soviet Union, removed 11 species from *Andricus* and transferred them again to reestablished *Adleria*. Their decision was based solely on the analysis of the adults of the asexual generations. The diagnostic characteristics given by these authors to separate *Adleria* from *Andricus* are the same as those in Weld (1952a). Kovalev (1965) described two other *Adleria* species from south of Far East of Russia, which were synonymized later to *Andricus* (Abe 1986). Currently the genus *Adleria* with 6 species is listed as a valid genus in Burks (1979) for America north of Mexico. Five of these species must be transferred to *Andricus*: *A. dimorphus* (Beutenmueller), **comb. nov.**, *A. flavicollis* (Ashmead), **comb. nov.**, *A. nigricens* (Gillette), **comb. nov.**, *A. quercustrobilanus* (Osten Sacken), **comb. nov.**, *A. vacciniiformis* (Beutenmueller), **comb. nov.**, and *A. weldi* (Beutenmueller), **comb. nov.**, while one species, *A. arizonica* (Cockerell) must be transferred to *Disholcaspis*: *D. arizonicus* (Cockerell), **comb. nov.** (the projecting part of the ventral spine of the hypopygium is shorter with very long setae reaching far beyond the apex of the spine, see *Disholcaspis*).

Weld (1951) synonymized *Andricus ashmeadii* Bassett to *Adleria nigricens* (Gillette). However, examination of the types showed an appreciable difference: in *A. ashmeadii* the ratio of antennal segments 1:3:4 is 20:20:11; the gena are only slightly broadened behind the eye; anterior tentorial pits are much deeper; the frons punctate; the scutum is bare with fine sculpture; scutellar foveae are larger with sculptured bottom; the transscutal articulation continuous, while in *A. nigricens* the ratio of antennal segments 1:3:4 is 15:20:13; the gena are much broader behind the eye; the frons is dull, transversely rugose; the scutum is densely pubescent, with more dull sculpture; scutellar foveae are smaller with smooth shiny bottom; the transscutal articulation is interrupted medially; the areolet of the forewing is twice shorter than in *A. ashmeadii*. We believe that these are distinct species and consequently we restore species status for *Andricus ashmeadii* Bassett, **comb. rev., status nova**.

Erythres. The only character separating this genus from *Andricus* is the simple tarsal claw. Both known species, *E. hastata* Kinsey and *E. jaculi* Kinsey occur on red oaks and induce cone-like galls inside enlarged bud scales and form terminal clusters of aborted leaves and bracts that enclose a small, seed-like cell. Galls resemble those of *Dryocosmus floridensis* (Beutenmueller), *Andricus stropus* Ashmead, *A. quercusfoliatus* (Ashmead), and *A. fecundator* (Hartig). Thus, *A. hastata* (Kinsey) and *A. jaculi* (Kinsey) are **comb. nov.**

Liodora and Dros. Dalla Torre & Kieffer (1910) treated *Liodora sulcata* Foerster as the sexual generation of *Cynips quercusfolii* (Linnaeus), however, Weld (1930, 1951, 1952a) considered *Liodora* as a distinct genus. Kinsey (1937a) stated that *Dros* "includes some species which have previously been assigned to 'Andricus', 'Driophanta' [sic], etc. Its further limitation must await a monographic revision of the whole group". He also mentioned that the genus may be related to *Feron* and *Druon* which were synonymized by Weld (1952a) to *Andricus*. *Dros*, according to Kinsey (1937a), is most readily distinguished from these "other genera" by a head which is narrowed behind eyes, by a 14- or 15-segmented antenna, entirely smooth scutum and mesopleuron, widely separated, pear-shaped scutellar foveae, and by distinctive vase or urn-shaped galls. The only difference between *Liodora* and *Dros* is that the head in *Dros* is narrower than the thorax while in *Liodora* it is equal to the thorax (Weld 1952a). However, this character is insufficient to distinguish *Liodora* from *Dros*. *Dros viscidum* (Weld), for example, differs from *Liodora* only by having a polished scutum, while *D. sessile* (Weld) has an alutaceous and polished scutum. The two genera were also confusing for Weld. Weld (1952a) considered *caepula* (Weld) and *discale* (Weld) as *Dros* species, but later moved them to *Andricus*; *viscida* was described by Weld (1944) in *Liodora*, but later was transferred to *Dros*. *Dros atrimentum* (Kinsey) and *D. pedicellatum* (Kinsey) originally were described in *Andricus*. Dailey & Sprenger (1973a) moved *atrimentum* (Kinsey) from *Dros* to *Andricus*. The same character states found in *Dros* and *Liodora* are encountered in many European *Andricus* species as in for instance, *inflator* Hartig, and *gallaeurnaeformis* (Fonscolombe). The latter species induces urn-shape galls as well.

Evans (1972) determined that *Liodora dumosae* Weld is the sexual generation of *Andricus pattersonae* Fullaway. Rosenthal & Koehler (1971) were incorrect when they concluded that this species was the bisexual generation of *Andricus kingi* Bassett, the latter was described by Dailey & Menke (1980). Probably Rosenthal and Koehler had the sexual generation of *A. kingi*.

Liodora and *Dros* are distinguished easily from the sexual *Cynips* by the presence of a long ventral spine of the hypopygium, with short sparse setae, which never reach beyond the apex of the spine.

Consequently, three *Liodora* and 11 *Dros* species known from North America must be transferred to *Andricus*: *apiarum* (Weld), **comb. nov.**, *clarkei* (Bassett), **comb. nov.**, *comata* (Weld), **comb. nov.**, *amphorus* (Weld), **comb. nov.**, *atrimentus* Kinsey, **comb. rev.**, *moreliensis* (Kinsey) (Mexico), **comb. nov.**, *pedicellatus* Kinsey, **comb. rev.**, *periscellus* (Kinsey) (Mexico), **comb. nov.**, *perlentus* (Kinsey) (Mexico), **comb. nov.**, *petasus* (Kinsey) (Mexico), **comb. nov.**, *picatus* (Kinsey) (Mexico), **comb. nov.**, *repicatus* (Kinsey) (Mexico), **comb. nov.**, *sessilum* (Weld), **comb. nov.**, and *viscidus* (Weld), **comb. nov.**

Parandricus. The genus is known from one species, *P. mairei* Kieffer, 1906, described from China, and is known to induce catkin galls on oaks (Kieffer 1906). The location of types is unknown. We examined one male and one female labelled as "Hankow" which are deposited at the USNM, Washington, DC and are originated from the type series. Weld (1952a) differentiated *Parandricus* from *Andricus* in that females have an "abdomen in side view longer than high, ... and hind femur stout". In many sexual *Andricus* species, which induce catkin galls, both females and males have "stout" hind femur. In males, except that the hind femur is very short and stout, metatarsus is equal 2+3+4 tarsomeres; 5th is equal 1st in length (Weld 1952a). However, several *Andricus* males, e.g., *A. quercuscalicis* (Burgsdorf), *A. burgundus* Giraud, *Callirhytis blastophaga* (Ashmead) and others, have the same proportions of hind tarsomeres and are "stout." Consequently, the proportions of hind tarsomeres and length of hind femur vary markedly in the sexual *Andricus*. Thus, the diagnostic characters given for *Parandricus* are insufficient to treat it as a separate genus and, thus *Parandricus* is a **syn. nova** of *Andricus*, and *Andricus mairei* (Kieffer) is a **comb. nov.**

Trichoterus. One of the diagnostic characters offered to separate *Trichoterus* (for the type species *T. coquilletti* Ashmead) from *Andricus* is a 12-segmented antenna, F2 is equal or slightly longer than F1. *Andricus formosalis* Weld, for example, has F2 longer than F1, has enlarged gaster as in *coquilletti*; in *A. pattoni* (Bassett) F2=F1; the shape and proportions of the head, scutum, scutellum, central area of propodeum, the forewing venation, the ventral spine of the hypopygium are the same as in *coquilletti*. The females of the sexual generation of the European *A. gallaearnaeformis* (Fonscolombe) have F2=F1, the head is slightly broader than the mesosoma, the scutum is same as in *Trichoterus*. Three species are known as brachypterous: *coquilletti* (fully winged females known also), *frondeum* (Weld), and *tubifaciens* (Weld). Consequently, all 8 known species must be transferred to *Andricus*: *burnetti* Dailey & Sprenger (1983), **comb. nov.**, *californicum* (Beutenmueller), **comb. nov.**, *coquilletti* (Ashmead), **comb. nov.**, *frondeum* (Weld), **comb. nov.**, *perfulvum* (Weld), **comb. nov.**, *rotundula* (Weld), **comb. nov.**, *tubifaciens* (Weld), **comb. nov.**, and *vacciniifoliae* (Ashmead), **comb. nov.**

Biology. Alternation of generations is known. These species induce galls on all organs of oak trees, and the shapes and sizes of galls vary markedly. Life-cycles are known for numerous European species, however, we know little about the life-cycles of the American and Asian species.

Distribution. Holarctic.

Aphelonyx Mayr, 1881

Aphelonyx Mayr 1881: 29. Type species: *Cynips cerricola* Giraud, 1859. Type designated by Mayr (1881).

Diagnosis. Very closely resembles asexual *Andricus*, differs in antennae 2.0 times as long as head+mesosoma, notauli incomplete in the anterior 1/3, tarsal claws are simple, while in asexual

Andricus notauli usually complete, antennae are less than 2.0 times as long as head+mesosoma, tarsal claws are usually toothed.

Biology. Only the asexual generation is known.

Distribution. Four species are known: *Aphelonyx cerricola* (Giraud, 1859) from Western Palaearctic, *A. crispulae* Matsumura, 1920, *A. glanduliferae* Matsumura, 1920, and *A. acutissimae* Monzen, 1953 from Japan (Monzen 1953), however, the last three Japanese species must be revised.

Atrusca Kinsey, 1929

Cynips (*Atrusca*) Kinsey 1930: 276. Type species: *Cynips* (*Atrusca*) *dugesi* var. *simulatrix* Kinsey. Original designation. Weld (1952a) gave it genus status.

Diagnosis. The malar space lacks sulcus; the scutum is reticulate; the forewing possesses dark spots and/or dark stripes along veins, the radial cell is 2.0-2.5 times as long as broad, the 4th abscissa of Rs is strongly angulate (Fig. 31). The scutum and the pronotum laterally have dense setae; the projecting part of the ventral spine of the hypopygium is at least 3-4 times as long as broad, subapical setae always long and dense, reaching far beyond the apex of the spine. Most closely resembles *Cynips* (= *Antron* and *Besbicus*), however, differs in diagnostic characters given above. See also Diagnosis to *Cynips*.

Comments. On the basis of a short radial cell and the absence of a malar sulcus, five species from the *Sphaeroterus* genus herein are transferred into *Atrusca*: *A. carolina* (Ashmead), **comb. nov.**, *A. rydbergiana* (Cockerell), **comb. nov.**, *A. texana* (Ashmead), **comb. nov.**, *A. trimaculosa* (McCracken and Egbert), **comb. nov.**, and *A. unica* (Weld), **comb. nov.**; one *Xanthoterus* species, *A. pulchripenne* (Ashmead), **comb. nov.** Dailey and Menke (1980) indicated that *Antron clavuloides* Kinsey must be placed in *Xanthoterus*. In our opinion, it must be transferred to *Atrusca*: *A. clavuloides* (Kinsey), **comb. nov.** because the ventral spine of the hypopygium is long and the radial cell is short, the 2nd abscissa of Rs is strongly angulate.

Biology. Only asexual generations are known currently that induce rounded detachable leaf galls.

Distribution. North and Central America.

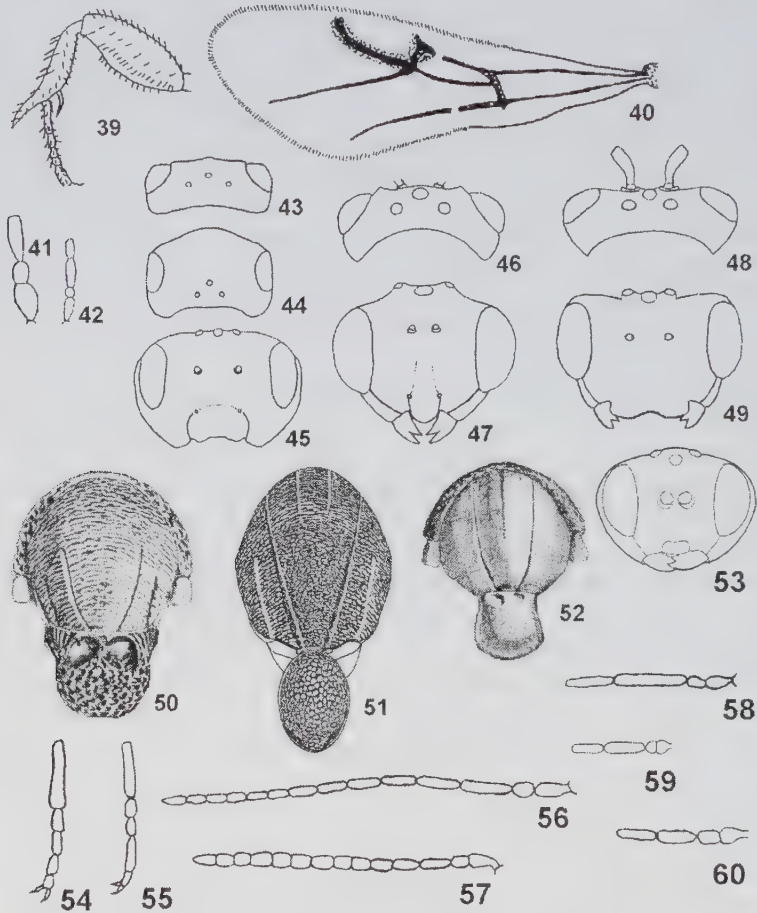
Bassettia Ashmead, 1887

Bassettia Ashmead 1887: 146. Type species: *Bassettia floridana* Ashmead, designated by Ashmead (1903). Types examined.

Diagnosis. Closely resembles *Plagiotrochus*, however, the head is 2.0-2.5 times as broad as long from above (Fig. 32), higher or equal to width in front view; the malar space lacks radiating striae (Fig. 33); the female forewing margin lacks cilia (Fig. 36); the median propodeal area is narrow, limited by nearly straight or slightly outward bent lateral propodeal carina, without or with fragmented median longitudinal carina (Fig. 37); F1 of the male antenna is nearly straight, not incised. In *Plagiotrochus*, the head is less than 2.0 times as broad as long from above (Fig. 34); as broad as high, or broader than high (transverse), but it is never higher than broad in front view; the malar space has radiating striae (Fig. 35); the female forewing margin has cilia; the central propodeal area is broad, limited by a strongly outward bent lateral propodeal carina, with complete or partially complete median longitudinal carina (Fig. 38); F1 of the male antenna is strongly incised and broadened distally. The asexual females of two *Bassettia* species (*B. ligni* Kinsey and *B. pallida* Ashmead) and one *Plagiotrochus* species (*Plagiotrochus australis* (Mayr)) share a

unique character within the Cynipini: the vertex has a deep longitudinal depression from the median ocellus to the antennal sockets, with or without a carina at the bottom.

Another closely related genus is *Loxaulus* Mayr, which can be easily distinguished from *Bassettia* by the structure of the propodeum similar to *Plagiotrochus* and the scutum is very finely transversely sculptured (Melika & Abrahamson 2000a).



Figures 39–60 39–40, *Belonocnema quercusvirens*: 39, fore leg, 40, forewing. 41–42, antenna, asexual female: 41, *Biorhiza pallida*; 42, *Trigonaspis quercusforticorne*. 43, *Cynips quercusfolii*, asexual female, head from above. 44–45, *B. pallida*, asexual female, head: 44, from above; 45, front view, asexual female. 46–49, *Trigonaspis megaptera*, sexual generation, head: 46, female, from above; 47, female, front view; 48, male, from above; 49, male, front view. 50–52, thorax, dorsal view: 50, *Callirhytis glandium*; 51, *Bassettia pallida*; 52, *Plagiotrochus quercusilicis*. 53, *C. glandium*, head, front view. 54–55, Hind tarsus: 54, *C. quercusfolii*, asexual female; 55, *B. pallida*, asexual female. 56–57, Antenna: 56, *C. quercusfolii*; 57, *B. pallida*. 58–59, first four segments of antenna: 58, *Disholcaspis quercusmamma*, female; 59, *D. quercusmamma*, male; 60, *Acraspis gemula*

Bassettia also resembles some *Callirhytis* species, however, the head is greater or equal to its width; the mesosoma is compressed dorso-laterally, usually 1.3-1.5 times as long as high in lateral view; the scutum 1.5-2.0 times as long as broad (Figs 32-33), while in *Callirhytis* the head is transverse, broader than high (Fig. 53); the mesosoma is arched, if slightly compressed dorso-laterally, then less than 1.2-1.3 times as long as high in lateral view; the scutum equal or only slightly longer than broad.

Comments. Four species from *Bassettia* must be transferred to *Callirhytis*: *C. aquaticae* (Ashmead), **comb. nov.**, *C. ceropteroides* (Basset), **comb. rev.**, *herberti* (Weld), **comb. nov.**, and *C. quercuscatsebaei* (Ashmead), **comb. nov.**

Biology. Alternate asexual and sexual generations are known. Rosenthal & Koehler (1971) and Evans (1972) described the sexual generation of *B. ligni* Kinsey. The present authors also found sexual *Bassettia* in Florida. The asexual generation induces stem galls with cells hidden under the bark of twigs. The sexual generation induces small oval swellings on leaves, which protrude both sides.

Distribution. Currently five *Bassettia* species are known, all from North America north of Mexico.

Belonocnema Mayr, 1881

Belonocnema Mayr 1881: 16. Type species: *B. Treatae* Mayr. Original designation. Types examined. Ashmead 1885 (synonym of *Dryorhizoxenus*).

Dryorhizoxenus Ashmead 1881: xxv. Type species: *D. floridanus* Ashmead. Original designation. Monotypic. Types examined. Ashmead 1886 (synonym of *Belonocnema*).

Diagnosis. Readily distinguished from all other Cynipini genera by the apex of the foretibia extending far beyond the base of the foretarsomere I (Fig. 39); 4th abscissa of Rs is strongly angulate, the forewing possess a short radial cell and narrow dark stripes prolong veins (Fig. 40).

Comments. It appears that *B. kinseyi* Weld, known to induce detachable pea-like leaf galls on *Q. virginiana* and distributed in Texas only, is the alternate generation of *B. treatae*, known to induce root galls on *Q. virginiana* and distributed from Florida and Georgia to Texas. Thus, *B. kinseyi* is a synonym of *B. treatae* (Lund, Ott & Lyon 1998). A congeneric species, *B. quercusvirens* (Osten Sacken) is known from Florida and Georgia only. Both species, *B. quercusvirens* and *B. treatae* (asexual generations) induce pea-like leaf galls on *Q. virginiana*, which are indistinguishable. However, in *B. quercusvirens* females, the spur on the foretibia is as long as the metatarsus, 2.0 times as long as the furcula; the midtibia possess a distinct spur, while in *B. treatae* the spur on the foretibia is 0.25 times as long as the metatarsus and is not longer than the furcula; the midtibia lacks a spur. So, it is questionable, if *B. quercusvirens* and *B. treatae* are distinct species or only different geographical races of the same species.

Biology. Recently alternation of generations for *B. treatae* Mayr was established experimentally (Lund, Ott & Lyon 1998).

Distribution. USA only (Florida, Georgia and Texas). Only two species are known.

Biorhiza Westwood, 1840

Biorhiza Westwood 1840: 56. Type species: *Cynips aptera* Fabricius, 1793. Designated by Westwood (1840).

- Apophyllus* Hartig 1840a: 185, 193. Type species: *Cynips aptera* Fabricius. Designated by Hartig (1840a). Mayr 1881 (synonym of *Biorhiza*). Monotypic.
- Teras* Hartig 1840a: 185, 193. Type species: *Cynips quercus terminalis* Fabricius, 1798. Designated by Hartig (1840a). Monotypic. Mayr 1881 (synonym of *Biorhiza*).
- Heterobius* Guérin-Meneville 1865: 138. Dalla Torre (1893), Dalla Torre & Kieffer (1910), Rohwer & Fagan (1917) (synonym of *Biorhiza*).
- Dryoteras* Foerster 1869: 331, 334. Type species: *Cynips quercus terminalis* Fabricius, 1798. Designated by Foerster (1869). Mayr 1881 (synonym of *Biorhiza*).
- Sphaeroterias* Ashmead 1897a: 67. Type species: *Biorhiza mellea* Ashmead, 1887. Designated by Ashmead (1897a). Mayr (1902), Beutenmueller (1909), Dalla Torre & Kieffer (1910) treated *Sphaeroterias* as a synonym of *Biorhiza*. Weld (1951) reestablished the validity of this genus. Types examined. **New synonym.**
- Beutenmueller (1909) erroneously treated *Xanthoterias* and *Phylloterias* also as synonyms of *Biorhiza*, while Dalla Torre (1893) and later Dalla Torre & Kieffer (1910) erroneously treated also *Philonix* Fitch as a synonym of *Biorhiza*.

Diagnosis. The asexual generation of *Biorhiza* most closely resembles *Trigonaspis*. Differs in having a more dorso-ventrally flattened mesosoma, the frons has longitudinal carina or elevation which reach between antennal sockets; F1 is only 1.2-1.5 times as long as F2 (Fig. 41); the scutellum does not or slightly overhangs the metascutellum; the dorsal median part of the pronotum is longer and more pronounced; the propodeum is nearly in the same plane as the rest of the mesosoma or only slightly declined; the projecting part of the ventral spine of the hypopygium is 1.0-1.5 times as long as broad, while in *Trigonaspis* the mesosoma is strongly arched anteriorly; the frons lacks elevation; F1 is 1.6-2.0 times as long as F2 (Fig. 42); the scutellum strongly overhangs the metascutellum; the pronotum is shorter in dorsal median line, the propodeum declines strongly, the projecting part of the ventral spine of the hypopygium is 2.0-2.5 times as long as broad.

The sexual generation of *Biorhiza* differs from *Trigonaspis* in that the head is straight between eyes from above, not lunate, ocelli smaller, the malar space without sulcus (Figs 43-45); scutellar foveae is absent, only a transverse groove is present anteriorly, while in *Trigonaspis* the head is lunate between eyes from above; ocelli larger; the malar space with deep sulcus (Figs 46-49); an indistinct ridge separates scutellar foveae, the bottom of which is smooth and shiny.

Some sexual *Andricus* females are very similar to *Biorhiza* but differ in that the hind tarsomer II is equal or longer than tarsomer V; the scutellum is smooth or delicately reticulate; antennae are filiform, antenna nearly equally broad through entire length, while in *Biorhiza* the hind tarsomere II is nearly 2.0 times as short as tarsomere V; the scutellum is dull rugose; antennae shorter, subsequent flagellomeres broadened to the apex.

Comments. *Sphaeroterias*. Ashmead (1897a) distinguished his newly described *Sphaeroterias* genus from "the true *Biorhiza* in having no carina on the frons between the antennae, in having only 13-jointed antennae, by the scutellum being rounded, and finally by the hind tarsi being much shorter than the tibiae." In the asexual generation of *Biorhiza pallida* Olivier, the first character varies extraordinarily from a distinct strong carina to a delicate elevation only. *Biorhiza nawai* (Ashmead, 1904) (= *B. weldi* Yasumatsu & Matsuda, 1955, synonym in Pujade-Villar, Ros-Farré & Melika 2002, *in press*) described from Japan also has a weak elevation only. *Biorhiza pallida* and *B. nawai* have 14-segmented antenna. However, even the type specimen of *S. melleum* has an indistinct suture that separates F11 from F12; antenna of one of the syntypes of Ashmead's

melleum has a distinct suture that separates F12. *Sphaeroterus caepuliforme* (Beutenmueller) has 14-segmented antenna. In *Biorhiza*, the shape of the scutellum varies from rounded to slightly elongated posteriorly; in some specimens the scutellum is more rounded than in the type specimen of *melleum*. In the majority of examined *S. caepuliforme* specimens, scutellum is slightly elongated posteriorly. The hind tarsus in the asexual *B. pallida* females is shorter than tibia; in the sexual females, which may be also apterous, the length of hind tarsus is nearly equal to the tibia. Weld (1951, 1952a) and later Burks (1979) placed 8 species into the genus *Sphaeroterus*. Only two of them belong to *Biorhiza*: *B. mellea* Ashmead, **comb. rev.** and *B. caepuliformis* Beutenmueller, **comb. rev.**, all other species must be transferred into *Atrusca*, based on the absence of the malar sulcus, short radial cell and strongly angulate Rs (see *Atrusca* above).

Sphaeroterus ocala (Weld) is known from Florida only and from the bisexual generation known to induce root galls on white oaks. It closely resembles asexual *Atrusca* because the forewing possesses dark stripes along veins, the radial cell is only 2.0–2.5 times as long as broad, the 2nd abscissa of Rs is strongly angulate. However, the ventral spine of the hypopygium is very short, less than 2.5 times as long as broad, which resembles the sexual *Cynips*. Thus, the status of this species is currently uncertain.

Also two species from *Xanthoterus* must be transferred to *Biorhiza*: *eburnea* (Bassett), **comb. nov.** and *emoryi* (Ashmead), **comb. nov.** (see also in *Trigonaspis* below).

Biology. Alternation of asexual and sexual generations is known.

Distribution. Holarctic. Six species are currently known: 4 from North America north of Mexico (herein transferred *Sphaeroterus* and *Xanthoterus* species), one species from Western Palaearctic and one species from Japan and Far East of Russia.

Callirhytis Foerster, 1869

Callirhytis Foerster 1869: 331, 335. Type species: *C. hartigi* Foerster. Original designation. Monotypic.

Eusymphagus Dettmer 1930: 54, 55, 56, 57. Type species: *E. bellus* Dettmer. Original designation. Dettmer 1933 (synonym of *Callirhytis*). Weld 1952a (synonym of *Andricus*, because tarsal claws with basal lobe). Nieves Aldrey 1992 (revision of the European species).

Diagnosis. A transversely rugose scutum characterizes only three Cynipini genera, *Bassetia*, *Callirhytis*, and *Plagiotrochus* (Figs 50–52). The diagnostic characters that separate *Callirhytis* from *Bassetia* and *Plagiotrochus* are discussed above (see Diagnosis to *Bassetia*). Additionally *Callirhytis* differs from *Plagiotrochus* in having a transverse head (front view), the malar space with a sulcus (Fig. 53); and forewing margins lack cilia. In *Plagiotrochus*, the head in front view is higher than broad, the malar space with radiating striae but without distinct malar sulcus (Fig. 35), and forewing margins are ciliate. The central propodeal area in *Callirhytis* is usually narrower than in *Plagiotrochus*, the latter in both generations has a very broad central propodeal area with strongly bent lateral longitudinal carinae, the area is usually smooth and delicately striate, except *P. marianii*, in which the central median area has strong parallel striae, but the area is large, broad.

Comments. Mayr (1881), Ashmead (1885), Cameron (1893), Dalla Torre (1893), Kieffer (1897–1901) and many others treated *Callirhytis* as a subgenus of *Andricus*, which differed in possessing simple tarsal claws, while the subgenus *Andricus* (*Andricus*) had tarsal claws with basal lobe. Mayr (1902) restored the generic status of *Callirhytis* and Dalla Torre & Kieffer (1910) followed this convention. The main diagnostic character for the reestablished *Callirhytis* genus was the simple tarsal claw. Weld (1930) wrote “in the original description of the genotype,

Callirhytis hartigi Foerster, it is not stated whether the tarsal claws are toothed." It is puzzling why no attention was given to the transversely rugose scutum; a diagnostic character of *Callirhytis* described by Foerster as the main diagnostic feature of the genus. As a consequence of misunderstanding the character's importance, the North American *Callirhytis* genus, in our opinion, currently includes more *Andricus* than *Callirhytis* species. Presence or absence of the basal lobes on tarsal claws is a specific nor a generic character. Nieves Aldrey (1992) in his revision of the European *Callirhytis* genus showed that different species vary in the presence or absence of toothed tarsal claws; for instance, both generations of *C. glandium* (Giraud) and the asexual *C. bella* (Dettmer) have tarsal claws with basal lobes, while other species have simple tarsal claws.

Of the 115 species placed into *Callirhytis* in North America north of Mexico (Burks 1979), only 15 species have the scutum transversely sculptured as in the typical Western Palearctic *Callirhytis* species: *cedrosensis* Dailey & Sprenger, *corrugis* (Bassett) (= *defecta* Kinsey), *eldoradensis* (Beutenmueller), *electrea* Weld, *flora* Weld (= *C. milleri*, the asexual generation (Dailey, Perry and Sprenger 1974), *fruticola* Ashmead, *fruticosa* Weld, *intersita* Weld, *lapillula* Weld, *medularis* Weld, *morrisoni* (Ashmead), *perrugosa* Weld, *petrina* Weld, *petrosa* Weld, *quercusmedullae* (Ashmead).

Two *Callirhytis* species, *quercuspomiformis* (Bassett) and *quercusrugosa* (Ashmead), herein are transferred to the *Amphibolips* genus (see *Amphibolips* above); all other species in our opinion belong to the genus *Andricus*.

Seven species of *Andricus* known from North America north of Mexico have the scutum transversely sculptured and, thus must be transferred into *Callirhytis* genus: *albobalani* (Weld), **comb. nov.**, *chrysobalani* (Weld), **comb. nov.**, *coortus* (Weld), **comb. nov.**, *coronus* (Beutenmueller), **comb. nov.**, *montezuma* (Beutenmueller), **comb. nov.**, *rhizoxenus* Ashmead, **comd. rev.**, and *wheeleri* (Beutenmueller), **comb. nov.**

Two species of *Bassettia* are transferred to *Callirhytis*: *ceropteroides* Bassett and *herberti* (Weld) (see *Bassettia* above).

Biology. Alternate asexual and sexual generations are known. The asexual generations are known to induce galls on/in acorns, while the sexual generations develop in stem swelling-like galls in young twigs or in cells hidden under the bark in twigs.

Distribution. Holarctic.

Chilaspis Mayr, 1881

Chilaspis Mayr 1881: 6, 32. Type species: *Andricus nitida* Giraud, 1882. Designated by Mayr (1881). Pujade-Villar, Ros-Farré & Melika (2002, *in press*) (revision of the genus).

Diagnosis. The genera *Cynips* and *Biorhiza* resemble *Chilaspis* in having a smooth mesoscutum and mesopleuron, but they possess malar sulcus, and the malar space lacks striae at the base of the clypeus. *Chilaspis* also resembles *Plagiotrochus*, however, it differs in possessing a smooth scutum and mesopleuron. *Chilaspis* is very closely related to *Dryocosmus*. In *Chilaspis*, striae on the frons are indistinct or weak, radiating from the clypeus in the malar space and in the lower face only; the vertex and occiput are smooth or very weakly coriaceous; the scutellum usually is uniformly smooth or weakly sculptured in the central part and occasionally with some wrinkles that prolong the marginal carina; scutellar foveae are separated by a distinct carina; the

pronotum is smooth in females, sometimes with indistinct striae in males, while in *Dryocosmus* striae radiate from the clypeus to one half of the eye height, some reaching the antennal foramina; the vertex and occiput are sculptured, sometimes strongly coriaceous or rugose; the scutellum is uniformly wrinkled; scutellar foveae are separated or not by a weak carina; the pronotum, especially in females, has long and distinct striae in the posterior lateral portion.

Closely related also to the genus *Cynips*, *Clilaspis* differs in the head, the scutum and scutellum are smooth and shiny, without reticulation, while in *Cynips* the scutellum and/or the head are reticulate or coriaceous.

Biology. Alternate asexual and sexual generations are known. The asexual generation emerges from rounded detachable leaf galls, while the bisexual generation develops in catkin galls.

Distribution. Three species are known from the Western Palaearctic only (Pujade-Villar, Ros-Farré & Melika 2002, *in press*). Known from Europe, North Africa, Israel, and Iran.

Cynips Linnaeus, 1758

Cynips Linnaeus 1758: 553. Type species: *Cynips quercus-folii* Linnaeus, 1758. Designated by Westwood (1840).

Dryophanta Foerster 1869: 331, 335. Type species: *Cynips quercus-folii* L. Designated by Foerster (1869). Monotypic. Rohwer & Fagan 1917 (synonym of *Cynips*).

Antron Kinsey 1930: 180. Type species: *Cynips (Antron) echinus* var. *schulthessae* form *schulthessae* Kinsey. Original designation. Weld (1952a) gave the genus status. Kinsey (1930) proposed as a subgenus of *Cynips*. Types examined. **New synonym.**

Besbicus Kinsey 1930: 222. Type species: *Cynips (Besbicus) multipunctata* var. *conspicua* Kinsey. Original designation. Weld (1952a) gave the genus status. Kinsey (1930) proposed as a subgenus of *Cynips*. Types examined. **New synonym.**

Diagnosis. Asexual females are fully winged; the ventral spine of the hypopygium is short, broadened at the apex, with dense, long subapical setae that reach far beyond the apex of the spine and form a dense truncate tuft (Fig. 15). Sexual females resemble those of *Biorhiza*, but differs in that the hind tarsomere II is equal or only slightly shorter than tarsomere V (Fig. 54); the head is narrower from above (Fig. 43), antennae filiform, subsequent flagellomeres of the same width (Fig. 56); the transscutal articulation is bent; the scutellum is longer, while in *Biorhiza* females the hind tarsomere II is shorter than V (Fig. 55); the head is broader from above (Fig. 44), antennae are shorter, subsequent flagellomeres broaden to the apex (Fig. 57); the transscutal articulation is straight; the scutellum is shorter. Males differ from *Biorhiza* in that they have F1 straight, not incised, while in *Biorhiza* F1 is strongly incised and enlarged distally. Males are also very similar to *Acraspis* and we are unable to find characters to distinguish them. See also Diagnosis to *Acraspis* and *Biorhiza*.

Comments. Mayr (1881) synonymized *Liodora* Foerster to *Dryophanta*. Dalla Torre (1893) treated it as a separate genus with one species, *L. sulcata* Foerster. Dalla Torre & Kieffer (1910) synonymized it with their "*Diplolepis* L. Geoffr." After revising Foerster's types of *L. sulcata*, Weld (1930) concluded that they are "not congeneric with the sexual generation of *Diplolepis folii* (L.)" and he restored it to generic status. See *Liodora* also above in *Andricus*.

Kinsey (1936) in his revision of the genus *Cynips* divided it into six subgenera: *Cynips* (European species), *Antron*, *Besbicus*, *Atrusca*, *Philonix*, and *Acraspis*. Under the "mellea" species-complex in the *Acraspis* subgenus, he included also all known *Sphaeroterias* species. It is

possible that *Acraspis* and *Philonix* might be synonyms of *Cynips*, however, more information on the alternation of generations is necessary. See also Diagnosis to *Acraspis* and *Atrusca*.

Antron and Besbicus. Weld's (1952a) key is incorrect in separating *Besbicus* from *Cynips* on the basis of structural differences in the ventral spine of the hypopygium (couplet 59). The structure of the ventral spine of both genera is identical (Fig. 19). The only diagnostic character given by Weld (1952a) for separation asexual generations of *Antron* and *Cynips* is the presence of smoky spots on forewing in *Antron* and their absence in *Cynips*. Kinsey (1936) described that the darker spotting on the forewings of *Cynips* (in his understanding of the genus) can vary strongly from no spots to numerous fused spots. Dark stripes along veins are typical for the European *Cynips* species. The peculiarities of Rs configuration, carinae on propodeum, width of genae, notauli completeness, and pubescence of the scutum, given by Weld (1952a) are specific rather than generic -level characters.

Alternation of generations occurs in *Antron* and *Besbicus*, however, the only *Besbicus* species known to have an alternate sexual generation is *B. mirabilis* (Kinsey) (Evans 1967). The adults of sexual *B. mirabilis* are entirely congeneric with the sexual generations of *Cynips*. Two species of *Antron* were listed among those with alternating asexual and sexual generations, *A. douglasii* (Ashmead) and *A. quercusechinus* (Osten Sacken). *Andricus ribes* Kinsey was listed as the sexual generation of *A. quercusechinus* (Weld 1951; Burks 1979). Weld (1952a) described for this species that "on circumstantial evidence this is considered the alternating generation of *echinus*". There is no evidence for this. Kinsey (1922a) did not mention that *A. ribes* might be the sexual generation of any other cynipid wasp in the original description. Kinsey (1930) gave no acceptable evidence for the synonymization of *A. ribes* to *A. quercusechinus*. However, *A. ribes* is entirely congeneric with sexual *Cynips* and, of course, is the sexual generation of one of the Californian *Cynips* (*Antron*) species. However, it is too early to state that it is the sexual generation of *A. quercusechinus*; this must be proved.

Weld (1951) and Burks (1979) listed *Dryophanta lobata* as the sexual generation of *Antron douglasii* (Ashmead), although, it was not mentioned in the original description (McCracken & Egbert 1922). Kinsey (1930) synonymized *A. lobata* to *A. douglasii* on circumstantial grounds. An examination of paratypes of females and a male [Paratype No. 53990, USNM] as well as the original description (McCracken & Egbert 1922) indicates that it is not a bisexual *Cynips*. There are no other bisexual cynipids known that have such broad, short ventral spines of the hypopygium. Consequently, the status of *D. lobata* is uncertain.

The following species must be transferred from *Besbicus* to *Cynips*: *conspicuus* Kinsey, **comb. rev.**, *heldae* Fullaway, **comb. rev.**, *indictus* Kinsey, **comb. rev.**, *leachii* Kinsey, **comb. rev.**, *maculosus* Weld, **comb. rev.**, *mirabilis* Kinsey, **comb. rev.**, *multipunctatus* (Beutenmueller), **comb. nov.**, *tritior* Kinsey, **comb. rev.**, as well as the following *Antron* species: *acraspiformis* (Weld), **comb. nov.**, *douglasii* (Ashmead), **comb. nov.**, *dumosae* Kinsey, **comb. rev.**, *magdalenae* (Weld), **comb. nov.**, *plumbeum* Weld, **comb. rev.**, *quercusechinus* Osten Sacken, **comb. rev.**, *quercusnubila* Bassett, **comb. rev.**, *russus* Kinsey, **comb. rev.** These species are known from North America north of Mexico. We have not analyzed *Besbicus* and *Antron* species mainly described from Mexico by Kinsey. They require a detailed revision.

We also transfer one species from the genus *Xanthoteras* to *Cynips*: *C. pulchellum* (Beutenmueller), **comb. nov.**

Biology. Alternation of asexual and sexual generations is known. The bisexual generation induces detachable leaf galls, while the asexual generation induces tiny small bud galls.

Distribution. Holarctic. One species, *Cynips staminobia* Kovalev, 1965, was described on the basis of males reared from catkin galls on *Quercus mongolica* from Far East of Russia (Kovalev 1965).

Disholcaspis Dalla Torre & Kieffer, 1910

Disholcaspis Dalla Torre & Kieffer 1910: 371. Type species: *Callaspidia quercus-globulus* Fitch, 1858.

Designated by Ashmead (1903). Types examined.

Holcaspis Mayr 1881: 35. Name preoccupied by Chaudoir in Coleoptera.

Diagnosis. Asexual females. Robust specimens, the ventral spine of the hypopygium is short, the projecting part is a maximum of 2.0-3.5 times as long as broad or much shorter, subapical setae are long, dense, reaching far beyond the apex, but never forming a dense truncate tuft; notauli incomplete; usually scutellum has a transverse impression anteriorly, scutellar foveae absent, if present then indistinct. See also Diagnosis to asexual *Andricus*. Sexual generation. The mesosoma is bare, with setae on the pronotum laterally only; the head is narrower than the mesosoma; the scutum anteriorly is microreticulate or coriaceous; the scutellum is elongated, gradually and very slightly depressed toward the transscutal articulation, without foveae or transversal groove; in females, F1 is 1.6-1.8 times as long as scapus+pedicellum, in males, F1 is 2.0 times as long as scapus+pedicellum (Figs 58-60). See also Diagnosis to sexual *Acraspis* and *Cynips*.

Comments. There are seven known species of *Disholcaspis* from the western United States: *D. chrysolepidis* (Beutenmueller), *conalis* Weld, *corallina* (Bassett), *plumbella* Kinsey, *sulcata* (Ashmead), *truckeensis* (Ashmead), and *washingtonensis* (Gillette), which differs from other species of this genus by the ventral spine of the hypopygium that is broad throughout its entire length, not tapering to a point at the apex; length of the projecting part of the spine is less or equal to its width; Rs is slightly curved in the apical one third and slightly expanded, median propodeal carinae bent, lyre-shaped, while in all other *Disholcaspis* species, the ventral spine is longer, needle-like, the projecting part at least 2.0-3.5 times as long as broad, Rs is straight, the radial cell is slightly longer; propodeal carinae are fragmented or lacking entirely.

Examination of types of some North American asexual *Andricus* species showed that there are three species: *lasius* (Ashmead), *reniformis* McCracken & Egbert, and *spectabilis* Kinsey; and also one *Adleria* species known from Mexico, *lapiei* (Kieffer) (= *Holcaspis weldi* Beutenmueller, 1911, not *Cynips weldi* Beutenmueller, 1918), which differs from "typical" *Disholcaspis*, *Andricus*, and *Adleria*. They agree in their morphology with the mentioned seven *Disholcaspis* species and form the same species-group.

This group of 11 species has caused problems in their placement. Weld (1952a) "provisionally placed in *Disholcaspis*" the seven *Disholcaspis* species mentioned above and wrote that "these species might well form a new genus if the life cycle of any one of them were known." Three *Andricus* species: *lasius*, *reniformis*, and *spectabilis* were "placed" in *Andricus*. Burnett (1977) placed 5 species (*conalis*, *corallina*, *plumbella*, *sulcata*, *washingtonensis*) in his new genus *Weldia* and described a new species, *californicus* (the name is not valid, since it was not published and the name *Weldia* was preoccupied by Yoshimoto (1962) for Eucolidae). On the basis of the presence of complete notauli, Dailey & Menke (1980) moved *truckeensis* to *Andricus*. Examination of a series of this species at the USNM indicated that notauli vary, notauli can reach the pronotum but also can disappear in anterior one third of scutum. *Andricus truckeensis* is similar to *lasius*, *reniformis*, and *spectabilis* in possessing a very short ventral spine of the hypopygium and all the

species occur on oaks of the subgenus *Protobalanus*. McCracken & Egbert (1922) suggested that *reniformis* might be a variety of *truckensis*. Dailey & Menke (1980) stated "additional studies may indicate that these four species should be placed in a new genus." Burnett (1977) considered *chrysolepidis* and *truckensis* as a distinct monophyletic group that forms a separate genus differing from the above mentioned seven *Disholcaspis* species. *Adleria lapiei* (Kieffer, 1911) originally was described in *Disholcaspis* (Kieffer 1911), but later Weld (1952a) "placed" it in *Adleria*. Kinsey (1937a) suggested that *D. lapiei* Kieffer was "probably a synonym of *D. weldi* (Beutenmueller)". A Weld note in the general collection of USNM included in a box containing *lapiei* Kieffer (= *Holcaspis weldi* Beut.), offers "Not a true *Disholcaspis*. Test Weld 1936" and later Weld (1952a) treated them as synonyms. Burnett (1977) provisionally treated *lapiei* as *Adleria*.

Consequently, the following species are transferred to *Disholcaspis*: *lasius* (Ashmead), **comb. nov.**, *reniformis* McCracken & Egbert, **comb. nov.**, *spectabilis* Kinsey; **comb. nov.**, and *lapiei* (Kieffer), **comb. nov.**

One species from the current North American *Adleria* is transferred herein to *Disholcaspis*: *arizonicus* (Cockerell), **comb. nov.** (see in *Andricus*).

Biology. Alternation of asexual and sexual generations is known. The sexual generation usually produces detachable, woody bullet-like stem and subterranean or root galls; the asexual generation induces small thin-walled bud galls of the same shape and structure as those of *Cynips*, *Acraspis* and many *Andricus*. For a long time only the asexual generation was known. Evans (1972) experimentally discovered the sexual generation of *D. eldoradensis* (Beutenmueller). We reared females and males from tiny pale grayish-white bud galls on *Quercus bicolor* Willd. collected in Pennsylvania (Bucknell Natural Area, Northumberland County, spring, 1996). Trees were heavily infested with galls of *D. quercusmamma* (Walsh) while other *Disholcaspis* species were not found in this area. The morphologies of these reared females and males agree with those of sexual *D. eldoradensis*. We believe these individuals represent the sexual generation of *D. quercusmamma*.

Distribution. North and Central America.

Dryocosmus Giraud, 1859

Dryocosmus Giraud 1859: 353. Type species: *D. cerriphillus* Giraud. Original designation. Monotypic. Pujade 1985 (revision of the Western Palaearctic species).

Entropa Foerster 1869: 330, 334. Type species: *E. lissonota* Foerster. Original designation. Monotypic. Mayr 1881 (synonym of *Dryocosmus*).

Diagnosis. Most closely resembles *Chilaspis*. Diagnostic characters for separation of *Dryocosmus* from *Chilaspis* are given in Diagnosis to *Chilaspis* above.

Comments. This genus needs a revision, especially the Nearctic and Eastern Palaearctic species; more precise and strict diagnostic generic limits must be established (Pujade-Villar, Ros-Farré & Melika 2002, *in press*).

Biology. The North American *Dryocosmus* species are morphologically uniform with the two known European species and with species described from Asia: *D. japonica* (Ashmead), *D. hakonensis* (Ashmead), *D. nawaii* (Ashmead), *D. mitsukurii* (Ashmead), and *D. kuriphilus* (Yasumatsu). The latter species threatened the chestnut industry of Japan and Korea and was discovered in Georgia, USA in 1974 (Payne 1978; Payne *et al.* 1975). This is the only species of

Cynipini known to associate with *Castanea*. Another species, known from Oregon and California, *Dryocosmus castanopsidis* (Beutenmueller) induces galls on catkins of *Castanopsis chrysophylla* and *C. sempervirens*. Several Eastern Palearctic species are known only from either asexual or sexual generation and probably some could be paired in alternate generations (Pujade-Villar 1985). Life cycles of these species must be identified in order to know the exact number of species and their limits.

Distribution. Holarctic distribution with 16 known Nearctic (Burks 1979), 2 Western Palearctic and 6 Eastern Palearctic species.

Eumayria Ashmead, 1887

Eumayria Ashmead 1887: 147. Type species: *E. floridana* Ashmead, 1887. Designated by Ashmead (1903).

Trisolenia Ashmead 1887: 142. Type species: *T. saltata* Ashmead, 1887. Designated by Ashmead (1903).

Rohwer & Fagan 1917 (name preoccupied by Ehrenberg in 1861 for Protozoa). Dalla Torre & Kieffer 1910 (synonym of *Andricus*).

Trisoleniella Rohwer & Fagan 1917: 377. New name for *Trisolenia*. Melika & Abrahamson 1997b (synonym of *Eumayria*).

Diagnosis. Head is 1.5-1.7 times broader than long from above in the sexual generation and is 2.5-2.8 times as broad as long in asexual females; malar sulcus absent (Figs 61-64); thorax is flattened dorso-ventrally, not arching in the anterior part; scutum is slightly longer than broad (Fig. 65), finely coriaceous or macroscopically punctate, never transversely sculptured; base of tergum II has pale felt-like ring of dense short setae, interrupted dorsally (in males dense short pale setae present only ventrally and ventro-laterally). See also the Diagnosis to *Eumayriella* Melika & Abrahamson below.

Comments. In Burks (1979), 4 species of *Eumayria* were listed, from which *Eumayria eldoradensis* was transferred into *Callirhytis* (Dailey *et al.* 1974) and *E. longipennis* to *Andricus*, as well as four species of *Trisoleniella* were transferred to *Eumayria* (Melika & Abrahamson 1997b).

Biology. Five species are known. *Eumayria floridana* Ashmead is known only from a bisexual generation and induces stem swelling-like galls, while the four other species have only asexual generations.

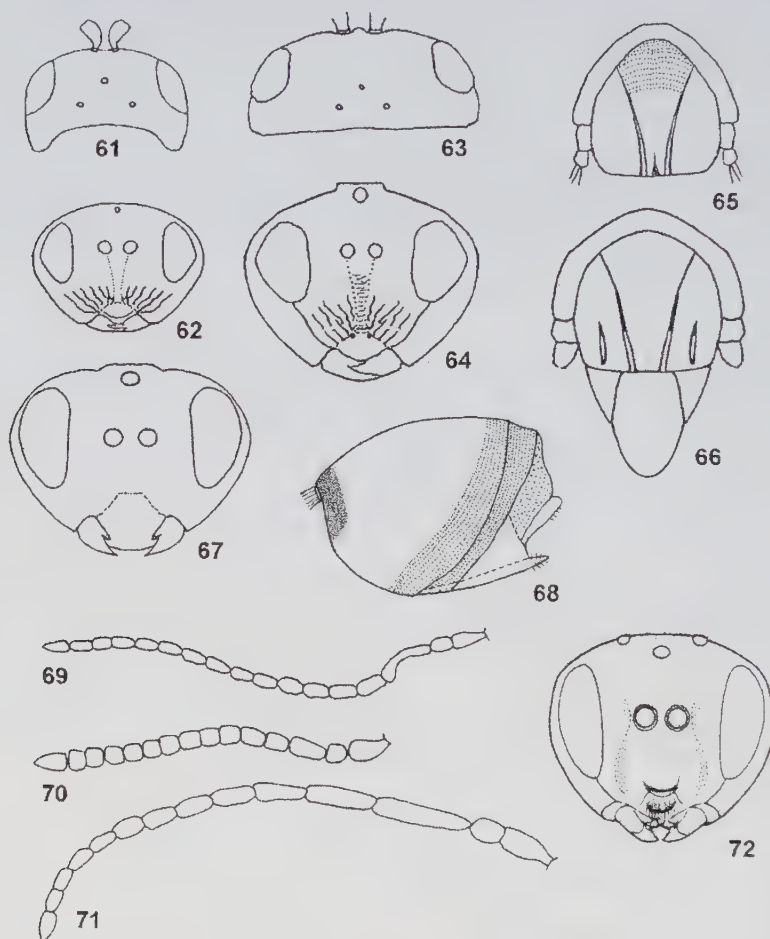
Distribution. Eastern and midwestern United States.

Eumayriella Melika & Abrahamson, 1997

Eumayriella Melika & Abrahamson 1997b: 672. Type species: *Eumayria invisa* Weld, 1952. Original designation.

Diagnosis. Closely resembles the brachypterous species of the former genus *Trichoteras* (*Andricus*, part, after authors, see *Andricus*). In *Eumayriella*, thorax is flattened dorso-ventrally; pronotum is dorsally much longer, placed in the same plane as scutum; scutum and scutellum are pubescent, each longer than broad, scutoscuteellar suture distinct, scutellum without foveae; head is broader than thorax from above, 2.3-3.0 times broader than high; antenna filiform, F2 shorter than F1; while in *Trichoteras* thorax is arched in anterior one-third; pronotum is much shorter dorsally and placed in a different plane than scutum; each scutum and scutellum is as long as broad; head is narrower or equal to thorax; antennae are short, F2 nearly equal F1. *Eumayriella* also closely

resembles *Eumayria*, but the head is more transverse in front view and from above (2.3-3.0 times broader than high, while in bisexual *Eumayria* it is only 1.5-1.7 times and in unisexual *Eumayria* – 2.5-2.8 times; malar space lacks radiating striae (Figs. 61-64, 67); antenna is filiform, long, 14-segmented, F1 substantially longer than pedicel and scape together; all flagellomeres are much longer than broad (Figs. 69-71).



Figures 61-72 61-62, *Eumayria floridana*, head: 61, from above; 62, dorsal view. 63-64, *E. enigma*, head: 63, from above; 64, dorsal view. 65-66, Scutum, dorsal view: 65, *E. floridana*; 66, *Eumayriella archboldi*. 67, *E. archboldi*, head, front view. 68, *E. floridana*, gaster. 69-71, Antenna: 69, *E. floridana*, male; 70, *E. enigma*, female; 71, *E. archboldi*. 72, *Loxaulus huberi*, head, front view

Scutum and scutellum are longer than broad, with dense white setae, without median and anterior parallel lines (Fig. 66); distinctly emarginated laterally and partially posteriorly as well; scutellum lacks foveae, with transverse depression along scutoscutellar suture; apical one third of

scutellum is gradually depressed toward apex and narrowed to a point that joins scutum along median dorsal part; posterior one third of scutellar disk is the highest part, strongly convex; sculpture of scutellar disk is very finely punctate, posterior one-fourth rugose. In *Eumayria*, head is nearly as high as broad, malar space and partially frons with radiating striae; antennae are much shorter, F1 as long as pedicel, scape as broad as long; F2 to F4 is slightly longer than broad, subsequent flagellomeres, except last one, subequal, nearly as broad as long; scutellum with foveae, posterior part of disk never convex; posteriorly rounded and has a dull rugose sculpture; scutum and scutellum are bare, without dense white setae. Second abdominal segment in *Eumayriella* lacks pale felt-like ring of dense short setae at base, while *Eumayria* has such a ring (Fig. 68). The latter character is used also to separate several genera of Eucoilidae (Quinlan 1986) and Figitinae (Figitidae) (Fergusson 1986).

Biology. Only asexual females are known. Galls are cell clusters, hidden under the bark of twigs. Two species, *E. archboldi* Melika & Abrahamson and *E. invisa* (Weld, 1952) represent this genus.

Distribution. Florida, USA.

Heteroecus Kinsey, 1922

Heteroecus Kinsey 1922b: 81. Type species: *Andricus dasydactyli* Ashmead, 1896. Designated by Kinsey (1922b).

Diagnosis. The only diagnostic character provided by Kinsey (1922b), to differentiate this genus from *Andricus* is the tarsal claws without lobe. Discovery of the alternation of generations in this genus (Lyon 1963, 1984) furnished more evidence to synonymize *Heteroecus* to *Andricus* or North American "*Callirhytis*" (sensu Weld 1952a).

Comments. Kinsey (1922b) wrote "Whether to interpret this group as a species or a genus is largely a matter of individual opinion and convenience." The validity of this genus is very dubious and might be synonym of *Andricus*, if the presence or absence of tooth on the tarsal claw is regarded as a non-generic character.

Biology. The other peculiarity of this genus is that the representatives of this genus are distributed in California only and are associated only with *Quercus chrysolepidicola*.

Distribution. California, USA. Twelve species were listed by Burks (1979). Later few new species were described, all from California (Dailey & Sprenger 1983; Lyon 1984). Thus, currently 16 species are known.

Holocynips Kieffer, 1910

Holocynips Kieffer 1910: 114. Type species: *H. emarginata* Kieffer. Original designation.

Diagnosis. The only distinction of *Holocynips* from many species of *Andricus* is the simple tarsal claw. All other diagnostic characters are found in many *Andricus* species.

Comments. The validity of this genus is very dubious and might be a synonym of *Andricus*, if the presence or absence of tooth on the tarsal claw is regarded as a non-generic character.

Biology. The asexual generation only is known. Galls are on roots or at the base of young sprouts on white oaks only.

Distribution. Four species are known: two from the Eastern and 2 from Western Coast of the USA.

Loxaulus Mayr, 1881

- Loxaulus* Mayr 1881: 9, 12, 33. Type species: *Cynips quercus-mammula* Bassett, 1881. Designated by Ashmead (1903). Monotypic. Melika & Abrahamson 2000a (revision of the genus).
- Solenozopheria* Ashmead 1887: 149. Type species: *S. vaccinii* Ashmead. Original designation. Monotypic. Weld 1951 (synonym of *Loxaulus*).
- Compsodryoxenus* Ashmead 1896: 128. Type species: *C. maculipennis* Ashmead, 1896. Designated by Ashmead (1903). Weld 1951 (synonym of *Loxaulus*).

Diagnosis. The head from above is broader than the mesosoma; the gena possess a malar sulcus (Fig. 72). The scutum is usually finely transversely coriaceous; the scutellum lacks foveae, with a transverse shallow depression (Fig. 74). The central portion of the propodeum is narrow, limited by parallel or slightly outward bent lateral carinae and with a median longitudinal carina and/or longitudinal striae; the median longitudinal carina in some species is indistinct, fragmented but always present at least in anterior half (Fig. 75). The radial cell of the forewing is short and broad, not more than 2.5 times as long as broad (except *L. quercusmammula* with the radial cell 2.6–2.7 times as long as broad), the forewing margin of female with or without cilia, with brown, smoky spots (or stripes) along the areolet, 2r, Rs, and M. (Fig. 76). Tarsal claws lack tooth. The ventral spine of the hypopygium is short, slender or needle-like; subapical setae are short and sparse, do not reach beyond the apex of the spine and the prominent part is never more than 3.0–3.5 times as long as broad (Fig. 73). The propodeum is similar to that of the Mediterranean genus *Plagiotrochus* Mayr. However, in the latter, the central portion of the propodeum is much broader, and is limited by the strongly outward-bending lateral carinae (Fig. 38).

Biology. The genus includes 14 species (Melika & Abrahamson 2000a). Alternate asexual and bisexual generations are known only for *L. trizonalis* Weld.

Distribution. North America only.

Neuroterus Hartig, 1840

- Neuroterus* Hartig 1840a: 185, 192. Type species: *Neuroterus politus* Hartig, 1840. Designated by Ashmead (1903).
- Spathegaster* Hartig 1840a: 186. Type species: *S. petioliventris* Hartig. Original designation. Monotypic. Mayr 1881 (synonym of *Neuroterus*).
- Ameristus* Foerster 1869: 333. Type species: *Neuroterus politus* Hartig. Designated by Rohwer & Fagan (1917). Mayr 1881 (synonym of *Neuroterus*).
- Dolichostrophus* Ashmead 1887: 129. Type species: *Cynips quercusirregularis* Osten Sacken, 1861. Designated by Ashmead (1887). Dalla Torre 1893 (synonym to *Neuroterus*).
- Neuroterus* subgenus *Diplobius* Kinsey 1923: 27, 28–31, 35. Type species: *Cynips floccosa* Bassett, 1881. Original designation.
- Neuroterus* subgenus *Dolichostrophus* Kinsey 1923: 25, 28, 32, 78. Type species: *Cynips irregularis* Osten Sacken Original designation.
- Neuroterus* subgenus *Neospathegaster* Kinsey 1923: 28, 35, 121. Type species: *Cynips vesicula* Bassett, 1881. Original designation.
- Neuroterus* subgenus *Neuroterus* Kinsey 1923: 27, 128. The nominal subgenus of *Neuroterus*.
- Neuroterus* subgenus *Pseudoneuroterus* Kinsey 1923: 130. Type species: *Cynips macroptera* Hartig, 1843. Original designation.
- Neuroterus* subgenus *Spathegaster* Kinsey 1923: 28, 131. Type species: *Spathegaster petioliventris* Hartig, 1840. Original designation.

Neoneuroterus Monzen 1954: 33. Type species: *N. kashiyamai* Monzen. Original designation. **New synonym.**

Repentinia Belizin & Maisuradze, 1961. In Maisuradze 1961: 28. Type species: *R. lencoranica* Belizin & Maisuradze. Monotypic. Original designation. **New synonym.**

Diagnosis. The scutum is smooth, microreticulate, or alutaceous, shiny, emarginated posteriorly along dorso-axillar surface; transscutal articulation is strongly emarginated laterally, if uninterrupted then strongly curved, never straight (Fig. 14); the scutoscuteellar suture is deep, the scutellum lacks separated foveae; fully winged, the radial cell of forewing is elongated, narrow. Usually notauli are absent or only barely traceable, however, some European species have distinct notauli, at least in the posterior half, and one species, *N. lanuginosus* Giraud, has deep notauli reaching the pronotum. The main diagnostic character that separates *Neuroterus* from all other genera of Cynipini is the absence of the scutoscuteellar suture. See also in Melika, Stone & Csóka (1999).

Comments. Kinsey (1923) divided the genus into 6 subgenera. Subdivision is appropriate since the genus includes morphologically diverse species, however, some subgenera are hardly distinguishable. The genus *Neuroterus* requires revision, particularly of the North American and Eastern Palearctic species (particularly described from Japan). A number of new *Neuroterus* species and synonymizations were made recently on the North American species (Melika & Abrahamson 1997a).

***Neoneuroterus*.** The only diagnostic characters given by Monzen (1954) for separation *Neoneuroterus* from *Neuroterus* were: antennae are 14-segmented in females and 15-segmented in males; notauli distinct and complete; head and mesosoma glabrous and smooth; the ventral spine of the hypopygium is long and pointed. However, all these characters occur in Western Palearctic *Neuroterus* species as well (see the recent key to the Western Palearctic *Neuroterus* species in Melika, Stone & Csóka 1999). We also examined the types of *Neoneuroterus boni-henrici* (Dettmer, 1934) and found no substantial characters to separate this species from other *Neuroterus* species. Thus, two *Neoneuroterus* species are transferred to *Neuroterus*: *N. kashiyamai* (Monzen, 1954), **comb. nov.** and *N. boni-henrici* Dettmer, 1934, **comb. rev.** Later, Kovalev (1965) described other *Neoneuroterus* species from Far East of Russia: *N. spumeus* Kovalev, 1965 (sexual gen., galls on leaves), *N. nephroideus* Kovalev, 1965 (sexual gen., galls in buds), and *N. vernicosus* (asexual gen., galls unknown). The latter species must be transferred into *Trigonaspis*: *T. vernicosus*, **comb. nov.** Two other species, *N. spumeus* and *N. nephroideus* must be revised, their placement in *Neoneuroterus*, and thus in *Neuroterus*, is questionable.

***Repentinia*.** Maisuradze (1961) described this species from Azerbaijan and placed it near *Neuroterus*. The asexual females are known to induce stem swelling-like galls on twigs of *Quercus castaneifolia* CAM. Maisuradze (1961) mentioned that the new genus closely resembles *Neuroterus* and differs in that the head and mesosoma have a dense white pubescence, F1 is very short, nearly equal F2; lateral propodeal carinae are absent. Weld (1964, ms.) wrote, "Genus can not be placed in key – perhaps near *Trichagalma*." We examined the types of this species at the Zoological Institute in St. Petersburg (Russia) and found no substantial characters to separate it from *Neuroterus*. Moreover, all the diagnostic characters given by Maisuradze (1961) for *Repentinia* occur in some *Neuroterus* species, particularly in *N. macropterus* (Hartig, 1843). Analysis of type series of *Repentinia lencoranica* showed that it is a **syn. nova** of *N. macropterus*. This species is widespread in Europe on *Q. cerris* only, but it also has been found in Israel on *Q. ithaburensis* (Sternlicht 1968), and is known from Bulgaria (Vassileva-Samnalieva 1974),

Romania (Ionescu 1973), and we identified large series collected from Turkey and Iran (Lorestan). Thus, it is apparent that the distribution of this species includes a large distribution within the Western Palaearctic.

Neuroterus (Latuspina) Monzen, 1954: 35. Type species: *Neuroterus (Latuspina) stirps* Monzen, 1954: 35. Original designation. The only character given by Monzen (1954) to differentiate this subgenus and species from *Neuroterus* is that the projecting part of the ventral spine of the hypopygium is not normally pointed at the apex, but dilated "like a spatula". No *Neuroterus* species are known to have distally broadened ventral spine. Consequently, *Latuspina* cannot be placed into *Neuroterus*. Weld (1964, ms.) stated that he was unable to obtain the types and that Dr. Yasumatsu, whom he asked to look for types, didn't find them in Monzen collection. Until the types are revised, the status of *Neuroterus (Latuspina)* Monzen will remain uncertain.

Biology. Nearly 100 described species, many are known to have alternate generations. Usually induce tiny integral or detachable leaf galls, mono- or polythalamous, or integral stem and catkin galls. Some species have polymorphic galls.

Distribution. Holarctic.

Odontocynips Kieffer, 1910

Odontocynips Kieffer 1910: 112. Type species: *O. nebulosa* Kieffer. Original designation. Monotypic.

Diagnosis. Easily distinguished from all other Cynipini by the presence of a strong apical lobe on the hind tibia (Fig. 77). Otherwise, it is closely allied to *Andricus* and *Holocynips*.

Biology. One species, *O. nebulosa* Kieffer, 1910 is known from the asexual generation only. It induces root galls on white oaks. Recently details of the biology were described (Wilson, Lester & Edmonson 2000).

Distribution. USA.

Philonix Fitch, 1859

Philonix Fitch 1859: 783. Type species: *P. fulvicollis* Fitch, 1859. Designated by Ashmead (1903). Types examined. Ashmead 1903 and Beutenmueller 1909 (*Acraspis* is a synonym of *Philonix*). Dalla Torre & Kieffer 1910 (synonym of *Biorhiza*). Weld 1922 (*Acraspis* and *Philonix* distinct genera).

Diagnosis. Closely resembles *Acraspis*, see **Diagnosis** to *Acraspis*.

Comments. Kinsey (1930) transferred *Dryophanta pallipes* Bassett into *Philonix* and considered it as the sexual generation of *P. fulvicollis*. However, Kinsey provided no justification for this synonymy. Weld (1959) wrote that *P. pallipes* was "perhaps a synonym of *Acraspis gemula* (Bassett)". We compared the three specimens of *P. pallipes* (from Beutenmueller collection, USNM, Washington, DC) with the paratypes of the sexual generation of *A. gemula* and found no differences. *Philonix pallipes* is a **syn. nov.** of *A. gemula*. If *P. pallipes* (Bass.) is treated as an *Acraspis* species, there is no evidence that species of *Philonix* have alternate sexual generations. Several species of *Philonix*, described by Kinsey (1930, 1936) from Mexico must be revised.

Biology. *Philonix* species are associated with white oaks only. Galls induced by *Philonix* species differ from those of *Acraspis*. They are fleshy, soft, and globular, attached to the leaves, usually the undersides, with a thick wall covered with a short very dense, felt-like pubescence.

Distribution. North America and Mexico.

Phylloter Ashmead, 1897

Phylloter Ashmead 1897a: 67. Type species: *Biorhiza rubinus* Gillette, 1888. Designated by Ashmead (1897a). Monotypic. Dalla Torre & Kieffer 1910 (synonym of *Trigonaspis*). Beutenmueller 1909 (synonym of *Biorhiza*). Types examined.

Xystoter Ashmead 1897b: 260. Type species: *X. volutellae* Ashmead, 1897. Original designation. Monotypic. Lyon 1993 (synonym of *Phylloter*). Types examined.

Euxystoter Lyon 1993: 138. Type species: *E. campanulatum* Lyon. Original designation. Types examined.
New synonym.

Diagnosis. Ant-like, apterous or brachypterous but the forewing is not longer than the mesosoma. Similar to *Zopheroter*, however, the scutellum is not knobbed; the head is equal or even higher than broad in front view. *Phylloter poculum* (Osten Sacken) has a slightly elevated scutellum similar to *Zopheroter*, but not nearly as strongly elevated. See also *Diagnosis* to *Zopheroter*. Closely related to *Trigonaspis* but has a longer, needle-like ventral spine of the hypopygium, the propodeum is placed in the same plane as the rest of thorax or only slightly declined, while in *Trigonaspis* the projecting part of the ventral spine is nearly 3.0 times as long as broad, the propodeum declines strongly.

Comments. Lyon (1993) separated *Euxystoter* from *Phylloter* “by its simple tarsal claws”. The inadequacy of this generic character argues that *Euxystoter* must be a synonym of *Phylloter*. Thus, *Euxystoter campanulatum* (Lyon 1993) must be transferred to *Phylloter*, *P. campanulatum* (Lyon), **comb. nov.** If data are obtained on the alternate bisexual generations of *Phylloter*, it is possible that it will join *Trigonaspis*, forming only a group of species rather than a separate genus.

Biology. Asexual generation is only known. Induces small detachable leaf galls.

Distribution. Eight species are known from North America.

Plagiotrochus Mayr, 1881

Plagiotrochus Mayr 1881: 32. Type species: *Cynips quercus-ilicis* Fabricius, 1798. Designated by Ashmead (1903).

Fioria Kieffer 1903a: 31. Type species: *Callirhytis marianii* Kieffer, 1903. Original designation. Kieffer 1903b (name preoccupied by Silvestri in 1869 for Myriapoda).

Fioriella Kieffer 1903b: 95. Melika, Ros-Farré & Pujade-Villar 2001 (synonym of *Plagiotrochus*).

Diagnosis. The gena in the asexual female is broadened behind the eye; the clypeus with radiating striae, do not project as a distinct lamella between mandibles, the malar sulcus is absent; the mesopleuron is shiny, flat in the postero-dorsal margin and ventral area; the metasoma is compressed laterally; the scutellum is equal or only slightly longer than the metascutellum; the propodeum forms an obtuse angle with the scutellum; the lateral propodeal carinae are strongly bent outwards, with a more or less impressed median carina; the ventral spine of the hypopygium is thin, with short sparse white setae not forming an apical tuft. See also *Diagnosis* to *Bassetia*, *Callirhytis*, and *Loxaulus*. *Plagiotrochus* also resembles *Chilaspis*, however, the latter differs from the former by a smooth scutum and mesopleuron.

Comments. All the mentioned characters are not exclusive to the genus *Plagiotrochus* but the above combination does define this genus. Homoplasies are very common in Cynipini and it is very difficult to find an exclusive diagnostic character for a given genus of Cynipidae, which is not

shared with another genus or other genera. For example, the main diagnostic character for recognizing *Plagiotrochus* in the Palaearctic area is the presence of a median propodeal carina, which, however, is also present in some species of the Nearctic *Loxaulus* and *Bassettia* (Melika & Abrahamson 2000a). Another character, the longitudinal depression on the vertex with a median longitudinal carina, is present in some asexual females of *Plagiotrochus* but also in some North American species, e.g., *Bassettia ligni* Kinsey and *B. pallida* Ashmead.

Plesiomorphic traits of *P. semicarpifoliae* (Cameron) known from the Himalayan area suggest a Southeast Asian origin for *Plagiotrochus* and all the species known from the Mediterranean region are derived forms (Bellido, Ros-Farré, Kovalev & Pujade-Villar 2000).

Weld (1926) described one species, *P. suberi* from California, which induces stem galls on the introduced European cork oak, *Quercus suber*. Later, Esquivel & De Santis (1953) described another asexual species, *P. abdominalis*, from Argentina, which is also known to induce stem galls. Nieves-Aldrey (2001) in his Fauna Iberica suggested that both, *P. suberi* and *P. abdominalis* are synonyms of *P. amenti* Kieffer (asexual generation, described as *P. pardoi* Nieves-Aldrey, 1985). However, Pujade-Villar (1998) regarded *P. pardoi* as a distinct species from *P. amenti* and, thus decided that *P. suberi* Weld, 1926 is a valid name, while *P. abdominalis* Esquivel & De Santis, 1953 and *P. pardoi* Nieves-Aldrey, 1985 are synonyms. Bailey & Stange (1966) wrote of *P. suberi*, "the insect has been found in Switzerland and Portugal (where it probably originated) only in the past few years." This species life cycle has changed and its population occurs as asexual females only. A failure in a genetic regulatory switch from thelytoky to bisexuality may have resulted in the deletion of the sexual generation in geographic isolation. Geographic parthenogenesis, for example, is present in *Andricus mukaigawae* (Mukaigawa) and *A. targionii* Kieffer in Japan (Abe 1986).

Biology. Alternation of generations is known. The asexual generation usually induces stem galls, the cells of which are hidden under the bark of twigs, while the sexual generation usually induces catkin galls. Some species induce leaf galls.

Distribution. Mediterranean region (Southern Europe and North Africa) – 7 sexual and 7 asexual *Plagiotrochus* forms are known (Bellido, Ros-Farré, Kovalev & Pujade-Villar 2000). Nieves Aldrey (2001) listed 10 *Plagiotrochus* species for the Iberian Peninsula, one species, *P. vilageliui* Pujade-Villar, 2000 was described from Corsica (France) (Pujade-Villar, Villemant & Andrei-Ruiz 2000). One species, *P. marianii* (Kieffer) was recorded from Slovakia and Hungary (Ambrus 1974; Melika, Ros-Farré & Pujade-Villar 2001), one species, *P. semicarpifoliae* is known from the Himalayan area. Introduced to California and Argentina.

Trichagalma Mayr, 1907

Trichagalma Mayr 1907: 3. Type species: *T. drouardi* Mayr. Original designation. Monotypic.

Diagnosis. The ventral spine of the hypopygium is slender and very short, the projecting part broader than long, with sparse subapical setae, reaching beyond the apex of the spine; the metasoma is strongly compressed laterally to a knife-edge dorsally; the forewing is 1.7 times as long as the body, with dark spots, Rs straight, the radial cell very long and narrow, (Fig. 78); the mesosoma is densely pubescent; the propodeum is very short, without carinae. No other Cynipini is known to have such strongly compressed metasoma laterally. In general, the head and mesosoma resemble asexual *Cynips*, however, the absence of notauli, scutellar foveae and propodeal carinae and the laterally strongly compressed metasoma clearly differentiate

Trichagalma from *Cynips*. Absence of notauli and scutellar foveae; smooth mesosoma, strongly laterally compressed gaster, the short ventral spine of the hypopygium also resemble *Neuroterus*. However, the robust size, strongly arched and densely pubescent mesosoma differentiates the genus from *Neuroterus*.

Comments. Ashmead (1904) described *Dryophanta serratae* from Japan (Sapporo) on the basis of one female, reared by Dr. Matsumura from the gall collected from *Quercus serrata*. Later Mayr (1907) described his *T. drouardi*, which appeared to be a synonym of *D. serratae* Ashmead (Monzen 1954). Thus, the genus is known from only one robust species, *T. serratae* (Ashmead, 1904).

Biology. Asexual females only are known to induce detachable stem galls, similar to those of the European *Andricus serotinus* (Giraud).

Distribution. Known from Japan only.

Trigonaspis Hartig, 1840

Trigonaspis Hartig 1840a: 186. Type species: *T. crustalis* Hartig, 1840. Original designation. Monotypic.

Xanthoteras Ashmead 1897b: 262. Type species: *Biorhiza forticornis* Walsh, 1864. Designated by Ashmead (1897b). Specimens from the original Walsh's series examined. **New synonym.**

Belizinella Kovalev 1965: 49. Type species: *B. gibbera* Kovalev. Original designation. Types examined. **New synonym.**

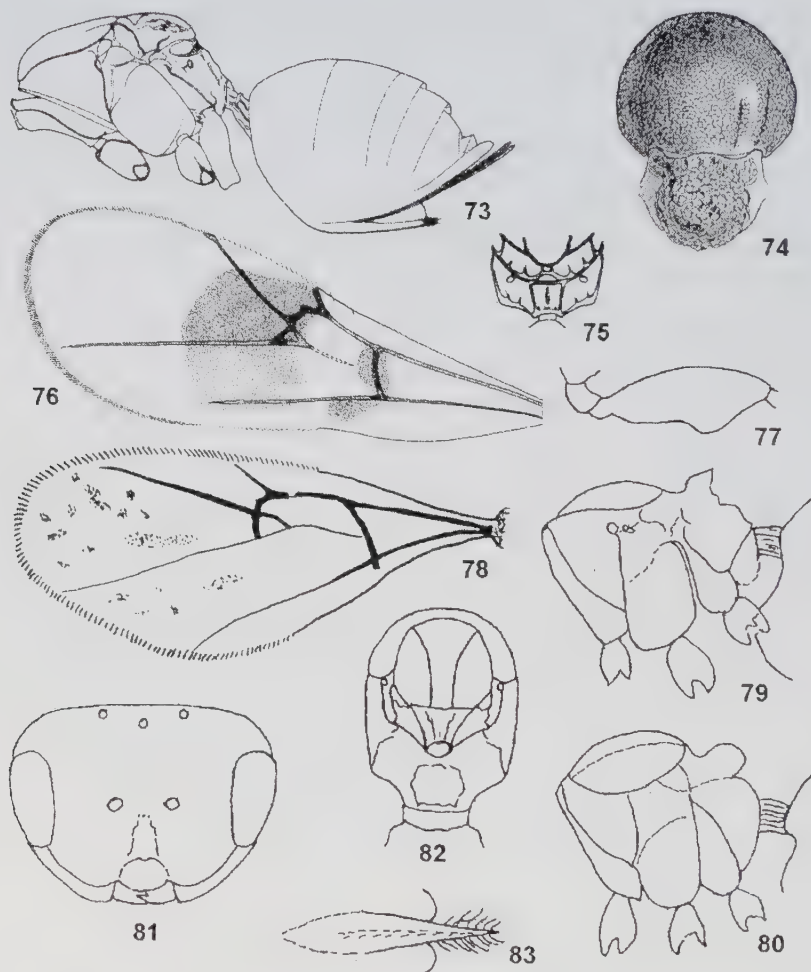
Ussuraspis Kovalev, 1965: 53. Type species: *U. nervosus* Kovalev. Original designation. Types examined. **New synonym.**

Diagnosis. *Trigonaspis* closely resembles *Biorhiza*, however, it differs in the presence of arched mesosoma and shorter pronotum. *Phylloteras* and *Zopheroteras* are also very similar to *Trigonaspis*, however they differ in having longer ventral spines in both genera, knobbed scutellum in *Zopheroteras*, and less arched mesosoma in *Phylloteras*. See also Diagnosis to *Biorhiza*, *Phylloteras* and *Zopheroteras*.

Comments. Dalla Torre & Kieffer (1910) treated *Zopheroteras* as a synonym to *Trigonaspis*. Beutenmueller (1909) placed *Xanthoteras* into *Biorhiza*, while Mayr (1902) considered *Xanthoteras* as a separate genus from *Biorhiza* (= *Sphaeroteras*) because of the strongly arched mesosoma and toothed tarsal claws. The original description of *Xanthoteras* (Ashmead 1897b) does not include substantial diagnostic characters to separate it from *Trigonaspis*. *Xanthoteras fumosum* (Weld), *X. pumiliventre* (Bassett), *X. radicola* (Ashmead) were described and are known from the sexual generations only. Although placed into *Xanthoteras*, they are congeneric with the European species, *T. megaptera* (Panzer). The sexual generation of *Trigonaspis* is quite different from that of *Biorhiza*, which earlier workers had synonymized as *Xanthoteras* (see Diagnosis to *Biorhiza*). Weld (1921) treated these three *Xanthoteras* species as *Trigonaspis* and only later transferred them to *Xanthoteras*.

Weld (1951, 1952a) and Burks (1979) placed 13 North American species into *Xanthoteras*. Dailey & Menke (1980) synonymized *X. obconicum* (Weld) to *X. pulchellum* (Beutenmueller). Seven *Xanthoteras* species here are transferred to *Trigonaspis*: *fumosa* Weld, **comb. rev.**, *mediocre* (Weld), **comb. nov.**, *ornata* Kinsey, **comb. rev.**, *pumiliventre* (Bassett), **comb. nov.**, *quercusforticorne* (Walsh), **comb. nov.**, *radicola* (Ashmead), **comb. nov.**, and *teres* (Weld), **comb. nov.** Two species, *X. eburneum* (Bassett) and *X. emoryi* (Ashmead) herein transferred to *Biorhiza*; *X. pulchellum* (Beutenmueller) is transferred to *Cynips*; *X. pulchripenne* (Ashmead) transferred to *Atrusca*.

Belizinella. Kovalev (1965) mentioned that his new genus is closely related to *Xanthoteras*, *Xystoteras* and *Trigonaspis* and from the latter, it differs in having a 14-segmented antennae, while in *Trigonaspis* antennae are 13-segmented (however, in *T. synaspis* antennae are 14-segmented). He mentioned also that in *Belizinella* notauli are absent, however, in *B. gibbera* the notauli are distinct and complete, reaching the pronotum. The galls of two newly described species *B. gibbera* and *B. vicina* are identical in their shape, location and inner structure as the gall of *T. synaspis*. Without doubt, it is a synonym of *Trigonaspis* and, thus, *Trigonaspis gibbera* Kovalev, **comb. nov.** and *T. vicina* Kovalev, **comb. nov.**



Figures 73–83 73, *Loxaulus huberi*, female, lateral view; 74, *L. masneri*, female, thorax, dorsal view; 75–76, *L. huberi*, female: 75, propodeum; 76, forewing. 77, *Odontocynips nebulosa*, hind tibia. 78, *Trichagalma serratae*, forewing. 79–80, Mesosoma, lateral view: 79, *Zopheroteras guttatum*; 80, *Z. sphaerula*. 81–82, *Z. guttatum*: 81, Head, front view; 82, mesosoma, dorsal view. 83, *Z. sphaerula*, ventral spine of hypopygium

***Ussuraspis*.** The diagnostic characters given by Kovalev (1965) for the separation of his newly described genus from *Trigonaspis* and *Xanthoteras* are not satisfactory – they are identical with those for *Trigonaspis*. So, *Ussuraspis nervosa* Kovalev, 1965 must be transferred to *Trigonaspis*: *T. nervosus*, **comb. nova**.

If data are obtained on the alternate sexual generations of *Phylloteras* and *Zopheroteras*, it may be that both genera will join *Trigonaspis* and will form only a distinct species groups rather than separate genera.

Biology. Alternation of asexual and sexual generations is known. Induces detachable leaf and root galls.

Distribution. Holarctic. We found undescribed *Trigonaspis* species from the material collected in China and Malaysia.

Zopheroteras Ashmead, 1897

Zopheroteras Ashmead 1897b: 261. Type species: *Acraspis vaccinii* Ashmead, 1887. Designated by Ashmead (1903). Dalla Torre & Kieffer 1910 (synonym of *Trigonaspis*).

Parateras Ashmead 1897b: 262. Type species: *P. hubbardi* Ashmead. Original designation. Monotypic. Weld 1922 (synonym of *Zopheroteras*).

Diagnosis. Ant-like, apterous or brachypterous species. Closely resembles *Phylloteras*, differs in that the scutellum is knobbed (Figs 79-80) and the head is transverse in front view (Fig. 81); the scutellum is elevated, with knobbed disk; notauli complete, strongly curving inward posteriorly (Fig. 82); the ventral spine of the hypopygium is narrow, needle-like, the projecting part is never less than 4-5 times as long as broad, subapical setae never reach beyond the apex of the spine (Fig. 83). Species are difficult to distinguish on the basis of the galls only. The adults are required for precise identification of the species.

Comments. If data are obtained on the alternate bisexual generations of *Zopheroteras*, it may be that it will join *Trigonaspis* and will form only a distinct group of species rather than a separate genus.

Biology. Only the asexual generation is known. It induces small, usually rounded or elliptic detachable leaf galls on both red and white oaks.

Distribution. Six species are known from North America (eastern and midwestern United States only).

Conclusions

From 41 currently valid genera 15 are synonymized. Thus, 26 genera in Cynipini are valid (Table 3). As the result, 73 **comb. nov.** and 26 **comb. rev.** are made.

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Table 3 Current arrangement of world genera of oak cynipid wasps (Cynipidae: Cynipini)

Proposed valid genera	New synonymic genera
1. <i>Acraspis</i> Mayr, 1881	<i>Paracraspis</i> Weld, 1952
2. <i>Amphibolips</i> Reinhard, 1865	
3. <i>Andricus</i> Hartig, 1840	<i>Dros</i> Kinsey, 1937, <i>Erythres</i> Kinsey, 1937, <i>Liodora</i> Foerster, 1869, <i>Parandricus</i> Kieffer, 1906, <i>Trichoteras</i> Ashmead, 1897
4. <i>Aphelonyx</i> Mayr, 1881	
5. <i>Atrusca</i> Kinsey, 1929	
6. <i>Bassettia</i> Ashmead, 1887	
7. <i>Belonocnema</i> Mayr, 1881	
8. <i>Biorhiza</i> Westwood, 1840	<i>Sphaeroteras</i> Ashmead, 1897
9. <i>Callirhytis</i> Foerster, 1869	
10. <i>Chilaspis</i> Mayr, 1881	
11. <i>Cynips</i> Linnaeus, 1758	<i>Antron</i> Kinsey, 1930, <i>Besbicus</i> Kinsey, 1930
12. <i>Disholcaspis</i> Dalla Torre & Kieffer, 1910	
13. <i>Dryocosmus</i> Giraud, 1859	
14. <i>Eumayria</i> Ashmead, 1887	
15. <i>Eumayriella</i> Melika & Abrahamson, 1997	
16. <i>Heteroecus</i> Kinsey, 1922	
17. <i>Holocynips</i> Kieffer, 1910	
18. <i>Loxaulus</i> Mayr, 1881	
19. <i>Neuroterus</i> Hartig, 1840	<i>Neoneuroterus</i> Monzen, 1954, <i>Reptinia</i> Belizin & Maisuradze, 1961
20. <i>Odontocynips</i> Kieffer, 1910	
21. <i>Philonix</i> Fitch, 1859	
22. <i>Phylloteras</i> Ashmead, 1897	<i>Euxystoteras</i> Lyon, 1993
23. <i>Plagiotrochus</i> Mayr, 1881	
24. <i>Trichagalma</i> Mayr, 1907	
25. <i>Trigonaspis</i> Hartig, 1840	<i>Belizinella</i> Kovalev, 1965, <i>Ussuraspis</i> Kovalev, 1965, <i>Xanthoteras</i> Ashmead, 1897
26. <i>Zopheroteras</i> Ashmead, 1897	

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PART 3

Molecular Phylogenetics and Systematics



MONOPHYLY AND PRELIMINARY PHYLOGENY OF ENTEDONINAE (HYMENOPTERA: CHALCIDOIDEA: EULOPHIDAE): 28S D2 rDNA CONSIDERATIONS AND MORPHOLOGICAL SUPPORT

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Abstract – Phylogenetic relationships of entedonine chalcid wasps (Hymenoptera: Chalcidoidea) were estimated based on D2 region of 28S rDNA gene. 76 species of Chalcidoidea representing 47 genera were included in the data matrix. 12 species from 8 entedonine genera were sequenced for the first time. The matrix included all known so far entedonine sequences (e.g. 5 species of Euderomphalini and 35 of Entedonini), 26 representatives of other Eulophidae and 10 species of outgroup taxa. The monophyly of both Eulophidae and Entedoninae is supported, but Euderomphalini are placed in a separate node together with Euderinae. All studied Entedoninae have first mesosomal spiracles hidden, invisible, and whole posterior edge of pronotum straight, generally overlapping the spiracle. To the contrary, the rest Eulophidae generally have the spiracles clearly visible, the pronotum with small to distinct incision around the spiracle, sometimes almost completely encircling it. This character represents the morphological support for the established monophyly of Entedoninae. All representatives of the tribe Euderomphalini have rather specific clypeus (delimited as a convex plate with incised anterior margin) and mandibles (with massive base and semi-circularly bent cutting margin). They share such shape of the clypeus with all known Euderinae. Such a congruence between molecular and morphological data resulted in placement of Euderomphalini in Euderinae. The latter subfamily is regarded as consisting of two tribes: Euderini Erdős, 1956 and Euderomphalini Schafee, Rizvi, Khan, 1988. Close relationships between the genera *Achrysocharoides* and *Entedon*, *Horismenus* and *Edovum*, *Ceraninus* and *Thripobius*, as well as taxonomic status of *Pediobius alcaeus*, and monophyly of some other genera is discussed in regard to both molecular and morphological data.

Key words: Eulophidae, Entedoninae, monophyly, cladistics, phylogeny, molecular sequencing

Introduction

The phylogeny of Eulophidae, a rather important group of insects, attracts significant attention in the last years. This family is the most numerous among the described families of Chalcidoidea (Noyes, 1978). They are widespread in the World, have one of the widest spectra of the trophic speciation, and many genera are of cosmopolitan distribution. Larvae of Eulophidae develop as ecto- and endoparasitoids of the hosts from the most insect orders, and occasionally also from Arachnida (spiders, mites) and nematodes (Gauthier *et al.* 2000).

Entedoninae is one of the 4 recognized subfamilies within Eulophidae (Gauthier *et al.* 2000). It includes more than 80 genera and about 500 species, but the real number of these taxa is hardly to be estimated now, because of both: poor study of the various faunas and shortcomings of the current systematics. Our preliminary studies demonstrate great numbers of taxa to be described, as well as lots of synonyms to be proposed.

Entedonine chalcid wasps are found in a variety of habitats, on all continents, except for Antarctica. Their larvae are endoparasitoids of Coleoptera, Diptera, Heteroptera, Hymenoptera,

Lepidoptera, Neuroptera, Thysanoptera, Orthoptera, Mantodea, and some other groups. Many of these hosts are of essential economical importance, what charges entedonines with considerable interest for biological pest control programs.

There are significant problems with the application of the current system of Entedoninae, their existing generic keys, reviews and taxonomical revisions. Unfortunately, generic concepts are prepared mostly for the Holarctic fauna, but weakly work even on regional level, being quite often useless for several regions (especially tropics). Another problem is that quite often there are no distinct hiatuses between genera, so that many new species either have no place in the current system, or are intermediate between the existing genera. Also there is clear disproportion in the value of the diagnostic characters — those proposed to be diagnostic for one genus occur in other genera as well, but are then treated as being of species-level only.

Previous data on phylogeny (historical overview)

The phylogeny of Entedoninae was discussed to different extents. Just twice it was reviewed exactly for the subfamily (Schauff 1991; LaSalle & Schauff 1994), also twice it was discussed at larger scale (Heraty *et al.* 1999; Gauthier *et al.* 2000). Bouček (1988) suggested that this group is certainly the most derived one among the four recognized subfamilies of Eulophidae (e.g. Eulophinae, Euderinae and Tetrastichinae). He stated: "... It seems to be derived from some ancestral forms close to the present Eulophinae, but not very close to Tetrastichinae or Euderinae... The phylogeny has hardly been studied and in many cases it is not clear which character states are primitive and which derived... The most ancestral form of venation is probably that of *Parzaommomyia*, a genus which seems to be related to *Omphale*."

The groundplan features for Entedoninae by Bouček (1988) were as follows (however, it was stated that some genera exhibit deviations from the basic pattern of characters):

1. Frontal grooves in an X-shape.
1. Notaular grooves on mesoscutum modified (not simply groove-like).
2. Scutellum with no paired grooves.
3. Scutellum with only one pair of setae.
4. Propodeum with simple spiracles placed near to metanotal margin and surrounded at least anteriorly by a groove, and postero-lateral corners reduced, often blunt, so that metapleuron is partly visible dorsally.
5. The forewing has the submarginal vein tapering distally, broken off from the broad base of parastigma, and bearing usually only 2 dorsal bristles.
6. The stigmal vein is mostly very short, also the postmarginal vein is frequently short though mostly distinct, only rarely absent.
7. The facial grooves include the frontal fork (= frontal sulcus) connected with more ventral scrobal grooves; the fork may be absent (*Entedon*), or transformed into a transverse groove or a transverse carina; the scrobal grooves are rarely indistinct, sometimes parallel in dorsal part (*Monteithius*).
8. The dorsal thorax has the pilosity mostly reduced to two pairs of setae on the median lobe of scutum (one pair only in about 10 genera) and one pair on the scutellum (with particular deviations).

Schauff (1991), when reviewing the Holarctic fauna, proposed a cladogram (Fig. 1) based on the analysis of 31 character and 25 taxa (genera), with eulophine genus *Sympiesis* as outgroup.

Schauff (1991) characterized Entedoninae by the combination of the mentioned below characters, while none of them strongly supported monophyly of this group, and all of them varied within the group:

1. Scutellum with a single pair of setae.
2. Male scape with sensory pores restricted to the ventral edge.
3. Submarginal vein with two dorsal setae.
4. Mesoscutal midlobe with two pairs of setae.
5. Possession of frontal grooves/sutures.
6. Subspiracular propodeal tubercle.
7. Marginal vein much longer than submarginal.
8. Stigmal vein short.
9. Submarginal vein broken.



Figure 1 The cladogram presented by Schauff (1991)

LaSalle & Schauff (1994) discussed the phylogeny of Entedoninae as well as monophyly of this subfamily when revising the genera allied to *Euderomphale* (in the tribe Euderomphalini). Schauff (1991) excluded *Euderomphale* from Entedoninae. However, this genus as well as six allied genera were regarded later as an entedonine tribe (following Shafee, Rizvi & Khan 1988) by LaSalle & Schauff (1994). In this work the checklist of characters proposed by Schauff (1991) was corrected and supplemented as following:

1. Scutellum with a single pair of setae.
2. Male scape with sensory pores restricted to ventral row.
3. Submarginal vein with two dorsal setae.
4. Mesoscutum with two pairs of setae.
5. Frontal sulcus (lines) present.
6. Subspiracular propodeal tubercle present.

and also (less valuable):

7. Submarginal vein broken.
8. Sstigmal vein short.
9. Marginal vein much longer than submarginal.

There were some works briefly discussing monophyly of Entedoninae and relationships of certain genera (for instance, Hansson 1996; Schauff 1985, 1986, 1987, 1988; Schauff, Yoshimoto & Hansson 1994; Schauff, LaSalle & Wijesekara 1998; Ubajdillah, LaSalle & Quicke 2000), but they referred mostly to the mentioned above works for the diagnoses of the subfamily.

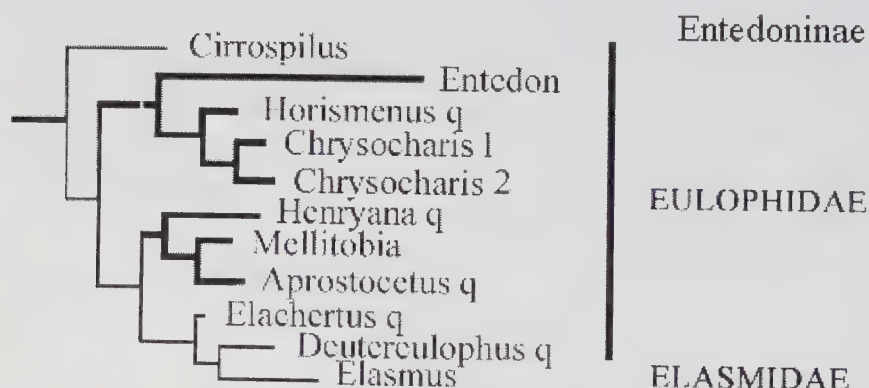


Figure 2 Fragment (with Entedoninae shown) of the cladogram presented by Campbell *et al.* (2000)

The first molecular application for the phylogeny of Entedoninae is that of Campbell *et al.* (2000) who overviewed the phylogeny of all Chalcidoidea (including Eulophidae and Entedoninae, in particular) based on 28S D2 region of rDNA. Entedoninae were monophyletic in this tree (Fig. 2), but represented by just a few taxa.



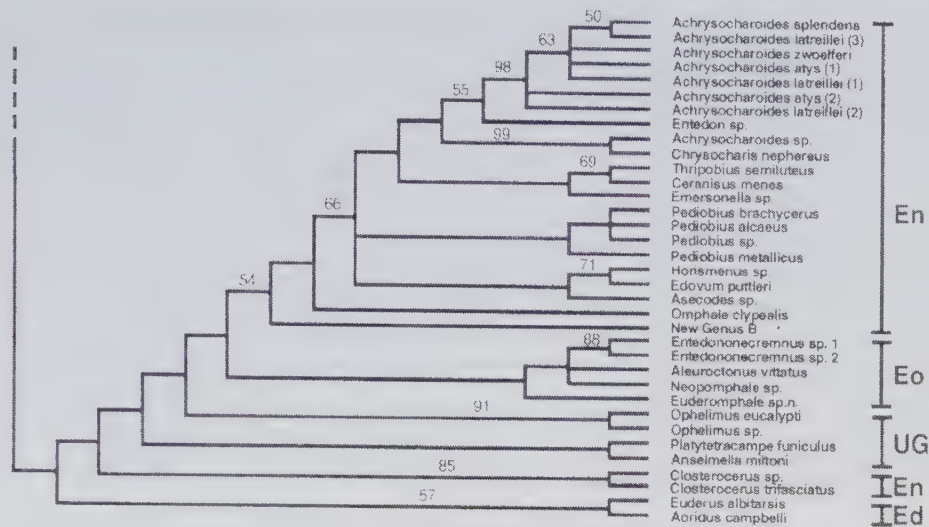


Figure 3 Fragment of tree presented by Gauthier *et al.* (2000).
En, Entedoninae; Eo, Euderomphalini; Ed, Euderinae; UG, unplaced genera

More informative data was proposed by Gauthier *et al.* (2000) under the analysis of the phylogeny of Eulophidae as a whole, based on the D2 region of the 28S rDNA. Entedoninae were represented by 29 species of 17 genera (including 5 species from 4 genera of Euderomphalini). In all 5 trees (Figs 3–6) proposed by Gauthier *et al.* (2000) and based on the different sequence

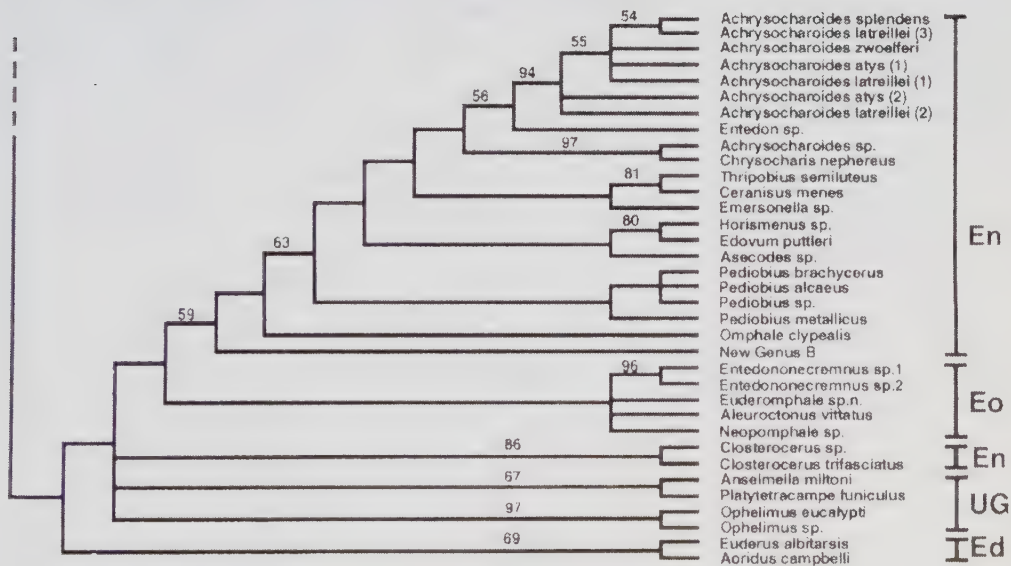


Figure 4 Fragment of tree presented by Gauthier *et al.* (2000)

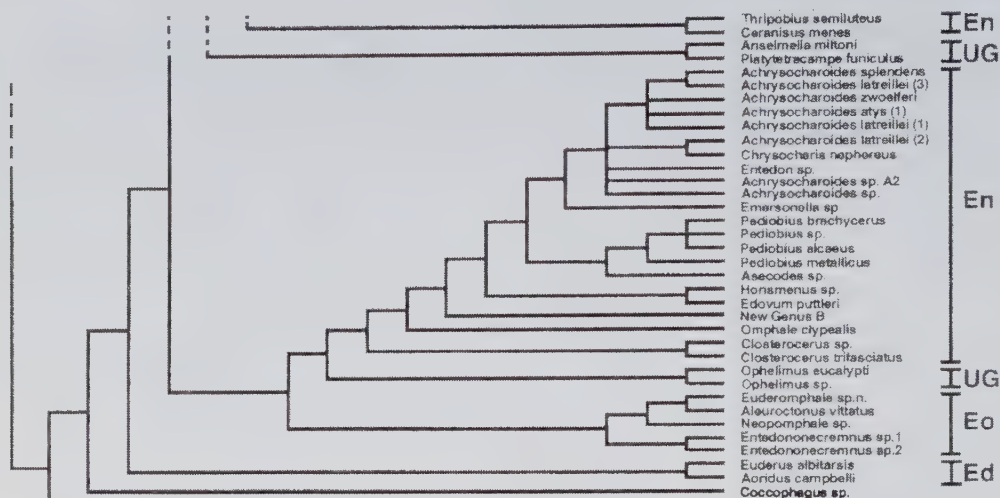


Figure 5 Fragment of tree presented by Gauthier *et al.* (2000)

alignment modes, both species of the genus *Closterocerus* ran out of the remainder of Entedoninae, and in one tree the tribe Euderomphalini represented a grade taxon. Despite that most of Entedoninae were monophyletic, low bootstrap support and neighborhood of the grade of Euderinae, Ophelimiini, Anselmeliini and Platytracampini, made such a monophyly somewhat “sensitive”.

The aim of my project was to trace phylogenetic relationships within Entedoninae based on a broader scale than it has been in previous work, and to find out whether there are any congruence between molecular and morphological data. Preliminary cladistic analysis of the morphological data set agrees largely with the phylogenetic pattern proposed below, and is a subject of the forthcoming publication.

Materials and Methods

Samples

Molecular data of the hitherto sequenced species were taken from EMBL/GenBank/DDBJ databases according to the accession numbers reported by Gauthier *et al.* (2000). 76 species representing 47 genera were used for D2 28S rRNA data set (Appendix 1). 12 species from 8 entedonine genera were sequenced for the first time (marked by * in Figs 8-9); all them are deposited in EMBL/GenBank/DDBJ databases (for accession numbers see Appendix 1). Rest sequences were retrieved from the EMBL and included in the matrix. So that the matrix included all known so far entedonine sequences (e.g. 5 species of Euderomphalini and 35 of Entedonini), 26 representatives of other Eulophidae (including representatives of the genera *Ophelimus*, *Anselmella* and *Platytracampe*, regarded as unplaced groups in Gauthier *et al.* 2000) and 10 species of outgroup taxa. The specimens of most newly sequenced species were collected personally by the author in Silwood Park and Windsor Great Park (England). The alcohol-preserved specimens of *Entedon* spp. from Bulgaria were kindly provided by Petr Boyadzhiev (University of Plovdiv “Paisii Hilendarski”, Plovdiv, Bulgaria).



DNA extraction, amplification and sequencing

Adult insects were killed directly in 70-95% ethanol. The Genomic DNA was extracted from single and/or two distinctly conspecific specimens using the DNeasy Tissue Kit (Qiagen) by crushing and incubating at 55°C for approximately 3-4 h in Proteinase K, with elution into 30 µl distilled water. Standard 50 µl PCR reactions were then carried out in an ABI 9600 thermal cycler using 1.0 µl DNA extract, 5 µl *Taq* buffer (1.5 mM MgCl₂), 1.5 U *Taq* polymerase (Roche), 10 nmol dNTPs (Amersham Pharmacia Biotech; APB) and 20 pmol of each primer. Primer sequences for PCR amplification of the D2 expansion region of 28S rDNA were: forward primer 5'-AGA GAG AGT TCA AGA GTA CGT G-3'; reverse primer 5'-TAG TTC ACC ATC TTT CGG GTC-3'. The GFX band prep. kit (APB) used in order to clean PCR products, which were then sequenced in both directions with the same primers using *Big Dye* terminator at half recommended volumes on an ABI 3700 automated sequencer. PCR condition were 35 cycles of 94°C denaturation (30 s), 45°C annealing (30 s) and 72°C extension (1 min) with an initial denaturation for 2 mins and final extension for 4 mins.

Sequence alignment

Sequences of each strand and those retrieved from EMBL/GenBank/DDBJ databases (Gauthier *et al.* 2000) were aligned using CLUSTAL W program (Thompson *et al.* 1994) by applying default settings and corrected manually if certain ambiguities were found (Appendix 2).

Phylogeny reconstruction

Phylogenies were reconstructed by the maximum parsimony analysis using PAUP* version 4.0d61 (Swofford, 1998) searching for optimum trees by swapping branches using a tree bisection reconnection (TBR) algorithm and storing a maximum number of equally parsimonious trees (MAXTREES) in memory. Two search strategies were used for better resolution of the phylogenies: unlimited and limited. The former suggested straightforward TBR with unlimited MAXTREES, while the latter, more quick, was based on limitation of the MAXTREES to 100. Heuristic search was carried out treating gaps as missing data, unweighted and unordered characters. A bootstrap analysis (100 replicates using TBR branch swapping) was carried out using PAUP* to establish levels of branch support for the clades obtained. The resultant consensus trees were viewed and stored by TREEVIEW program (Page 1996).

Results and Discussion

The manually aligned D2 28S rDNA sequences consist of 585 positions (see Appendix 2 on CD). Of these sites 190 were constant, 162 variable but parsimony-uninformative, and 233 (39.8%) parsimony-informative. The shortest tree found by both search strategies was of 1410 steps length, while the number of trees retained was 1818 for the unlimited and 100 for the limited search.

Figure 8 shows the strict consensus of 1818 trees found by the unlimited search (USC, tree length = 1451; the consistency index, CI = 0.4618; the homoplasy index, HI = 0.5382; CI excluding uninformative characters = 0.3712; HI excluding uninformative characters = 0.5382; the retention index, RI = 0.6582; the rescaled consistency index, RC = 0.3039). The strict consensus

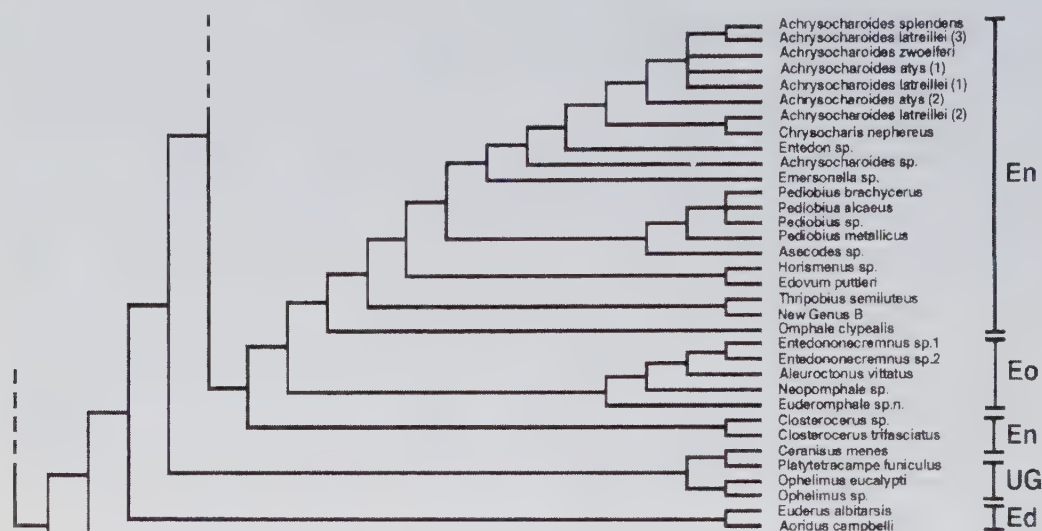


Figure 6 Fragment of tree presented by Gauthier *et al.* (2000)

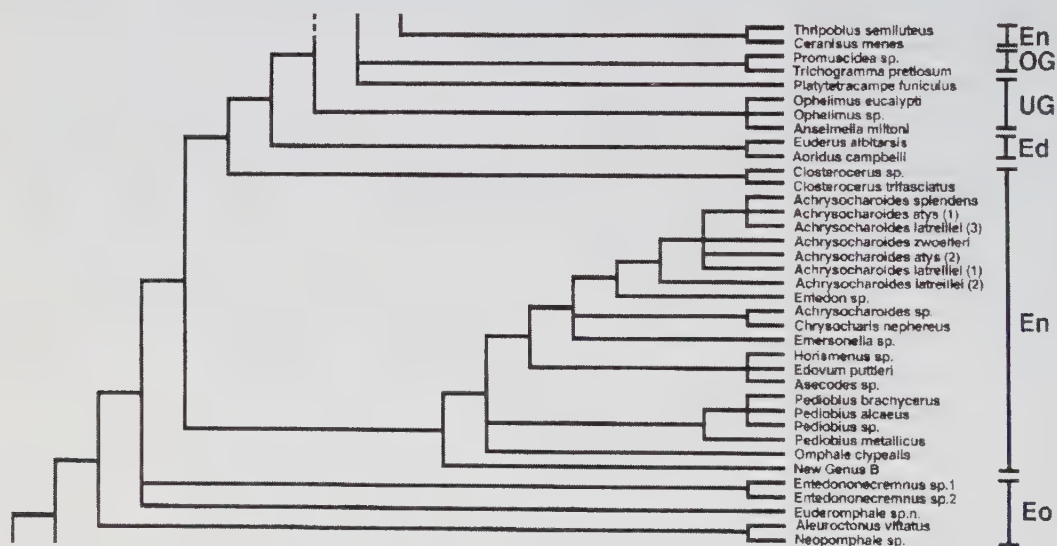


Figure 7 Fragment of tree presented by Gauthier *et al.* (2000)

tree of 100 trees obtained from the limited search is shown in Fig. 9 (LSC). It is shorter and its corresponding indices are slightly higher (tree length = 1425; CI = 0.4702; HI = 0.5298; CI excluding uninformative characters = 0.3791; HI excluding uninformative characters = 0.6209; RI = 0.6696; RC = 0.3148). Both analyses are in broad agreement in their overall topology, and differ only in monophyly of some traditionally recognized genera (e.g. *Entedon*, *Achrysocharoides*). The apomorphy list for the nodes of the strict consensus trees, corresponding to main monophyletic

entities, have been obtained from the tree description option of PAUP*, and presented in Table 1. Bold numbers below/above branches in Fig. 8 are bootstrap values. Abbreviations used in Figs 8, 9 follow those of Gauthier *et al.* (2000) and mean: OG, outgroups; EL, Eulophidae; UG, unplaced groups (but provisionally eulophids); EU, Eulophinae; Eu, Eulophini; Ci, Cirrospilini; TE, Tetrastichinae; EN, Entedoninae; ED, Euderinae; Ed, Euderini; Eo, Euderomphalini. For two species of *Closterocerus* their previous generic names are given (i.e. *Asecodes* and *Neochrysocharis*), because they have been submitted to EMBL/GenBank/DDBJ databases prior the publication proposing the synonymy of these generic names with *Closterocerus* (Gumovsky 2001a).

Monophyly of Eulophidae

In Gauthier *et al.* (2000) Eulophidae were not strictly monophyletic. In our tree they are monophyletic, however, the bootstrap estimate is not very high (62). There are no exact morphological characters showing monophyly of Eulophidae. The most promising characters were discussed in Gauthier *et al.* (2001). The present monophyly of this group, based on the molecular data set, should push forward the more intensive morphological research of the group as a whole.

Table 1 List of changes of respective sites D2 28S gene sequences supporting monophyly of main groups in both consensus trees: resulted from the unlimited search (USC, Fig. 8) and limited search (LSC, Fig. 9); bootstrap values are the same as in Fig. 8 (* CI means the Consistency Index for particular character)

Group	Tree type	Bootstrap value	Character	CI*	Change
Eulophidae	USC	63	100	0.1	t → c
			211	0.4	t → g
			213	0.333	c → t
			221	0.333	g → t
			289	0.2	c → g
			302	0.273	c → g
			311	0.4	c → a
			312	0.429	c → a
			317	0.667	g → t
			346	1	a → t
			372	0.167	g → a
			426	0.5	c → t
			532	0.667	c → a
			547	0.5	t → a
Entedoninae	USC		42	0.2	t → g
			124	0.2	t → c
			150	0.231	t → c
			289	0.2	t → a
			338	1	g → t
			349	1	t → a
			369	0.286	t → a
			432	0.4	t → a

Group	Tree type	Bootstrap value	Character	CI*	Change
Euderomphalini	USC		149	0.231	g → t
			302	0.273	g → t
			312	0.429	c → g
			327	0.667	c → t
			369	0.286	t → a
			464	0.083	c → t
			523	0.4	t → c
			524	0.286	c → a
			525	0.5	c → a
			547	0.5	g → t
Euderomphalini and Euderini	USC		548	0.286	a → t
			69	0.2	c → t
			87	0.333	c → t
			102	0.5	c → t
			103	0.5	g → c
			105	0.429	t → g
			106	0.286	c → t
			107	0.3	t → c
			219	1	c → t
			309	0.25	t → c
			322	0.333	g → a
			338	1	t → c
			355	0.333	g → a
			364	1	t → g
			382	1	a → c
			384	1	a → t
			464	0.083	t → c
			523	0.4	a → t
			525	0.5	a → c
			530	0.5	a → t
<i>Ceranisuus</i> -complex	USC	74	547	0.5	a → g
			38	0.286	t → c
			42	0.2	c → t
			49	0.273	t → c
			72	0.188	t → c
			123	0.2	t → g
			124	0.2	c → t
			150	0.231	a → g
			276	0.222	t → c
			289	0.2	t → g
			352	0.158	t → a
			353	0.182	t → a



Group	Tree type	Bootstrap value	Character	CI*	Change
<i>Entedon</i> + <i>Achrysocharoides</i>	USC	98	42	0.2	c → t
			107	0.3	t → c
			128	0.25	t → c
			142	0.154	t → c
			149	0.231	t → c
			150	0.231	a → g
			478	0.067	c → t
<i>Achrysocharoides</i> (most)	USC	98	490	0.214	a → g
			99	0.5	c → t
			142	0.154	c → t
			144	0.333	c → t
			234	0.222	c → a
			289	0.2	t → c
			370	0.2	t → c
<i>Entedon</i>	LSC	70	381	0.25	t → c
			490	0.214	g → a
			142	0.286	t → c
<i>Horismenus</i> + <i>Edovum</i>	UCS	70	490	0.250	a → g
			72	0.188	t → c
			224	0.333	t → c
			300	0.25	a → c
<i>Pediobius</i>	LSC	70	450	0.125	c → t
			523	0.4	a → c
			42	0.231	t → c
			43	0.4	c → a
<i>Pediobius alcaeus</i> rest of <i>Pediobius</i>	LSC	70	142	0.286	t → c
			150	0.25	g → a
			478	0.077	c → t
	LSC	70	72	0.214	t → c
			303	0.333	t → c

The representatives of Anselmelini, Ophelimini and Platytetracampini, all together, represent a sister group to Tetrastichinae and Eulophinae (bootstrap estimate 93%). It was Bouček (1988) who put *Anselmella*, *Ophelimus* and *Platytetracampe* in Eulophidae, however, there was no mutual grouping of these taxa in Gauthier *et al.* (2001), so that this placement was considered doubtful. These groups are of Australasian distribution and have more antennal segments than the rest of Eulophidae, what may be an indirect support for the monophyly of this group. According to the pattern in Figs 8 and 9, this group may be accorded subfamilial status within Eulophidae. Anyway, a futher study of the morphology of the representatives of Anselmelini, Ophelimini and Platytetracampini will support or disprove such a placement.

As to the question about the most primitive eulophid group, our data show, in general agreement with Gauthier *et al.* (2000) that this is Euderinae (but in a new concept, see below).

Monophyly of Entedoninae

Entedoninae are monophyletic in the trees obtained (Figs 8, 9, Table 1). The best morphological character supporting such a monophyly is the hidden first (fore) mesosomal (= mesothoracic, = prothoracic) spiracle (Fig. 10). The structure of this spiracle has never been discussed earlier for Eulophidae. Gibson *et al.* (1997) mentioned that the spiracle "is along the anterolateral margin of the mesoscutum, typically at or near the juncture formed between the mesoscutal margin, the pronotum, and the anterodorsal angle of the prepectus; rarely the spiracle is surrounded by pronotal cuticle when the prepectus is fused with pronotum".

The structure of the spiracle is one of the best characters separating Chalcidoidea from Platygastroidea; it is separated from the mesopleuron by the prepectus in the former group and is placed between the pronotum and the mesopleuron in the latter group. In part of platygasteroids the spiracle is placed on the pronotum. Graham (1987) in the character matrix proposed by him, subdivided the first mesothoracic spiracle (called pronotal) into two conditions: "not projecting" [0] and "projecting slightly, as seen in dorsal view" [1]. There was no further development of these definitions, as well as any phylogenetic or diagnostic implications.

In Platygastroidea (regarded as more ancient group than Chalcidoidea by (Rasnitsyn 1980)) the spiracle is placed entirely at the pronotum in Platygastriidae and closely to pronotum in Scelionidae.

The structure of the spiracle in various groups of Chalcidoidea requires a special attention and classification. In most studied Chalcidoidea the form of the spiracle is typical for the entire superfamily, e.g. a small exposed circle placed between the pronotum and the prepectus, with no shift to pronotum. There are some exceptions, e.g. in Eurytomidae and some Torymidae (having these spiracles hidden) what may be an independent case.

As to basal Chalcidoidea, most (if not all) Mymaridae have the spiracles exposed, placed at the pronotum and sometimes stalked, e.g. the genera *Neomymar* Crawford and *Ptilomymar* Annecke and Doutt (see Figs 110, 137, 143, 147, 150, 158, 167, 181, 185 in Yoshimoto 1990). It is interesting that in part of Mymaridae (including those with first mesosomal spiracles stalked) the tarsi are 4-segmented like in most Eulophidae.

The shape of first mesosomal spiracles is useful for the diagnosis of Entedoninae since all studied representatives of the subfamily have the spiracles hidden, invisible, and whole posterior edge of pronotum straight, generally overlapping the spiracle (Fig. 10d, framed). To the contrary, Eulophinae, Tetrastichinae and Euderinae have the spiracles clearly visible, the pronotum with small to distinct incision around the spiracle, sometimes almost completely encircling it (Figs 10a, 10b, 10c).

In view of above-mentioned considerations, I regard exposed, encircled by the pronotum, first mesosomal spiracles as plesiomorphy within Eulophidae, and hidden spiracles as synapomorphy for Entedoninae.

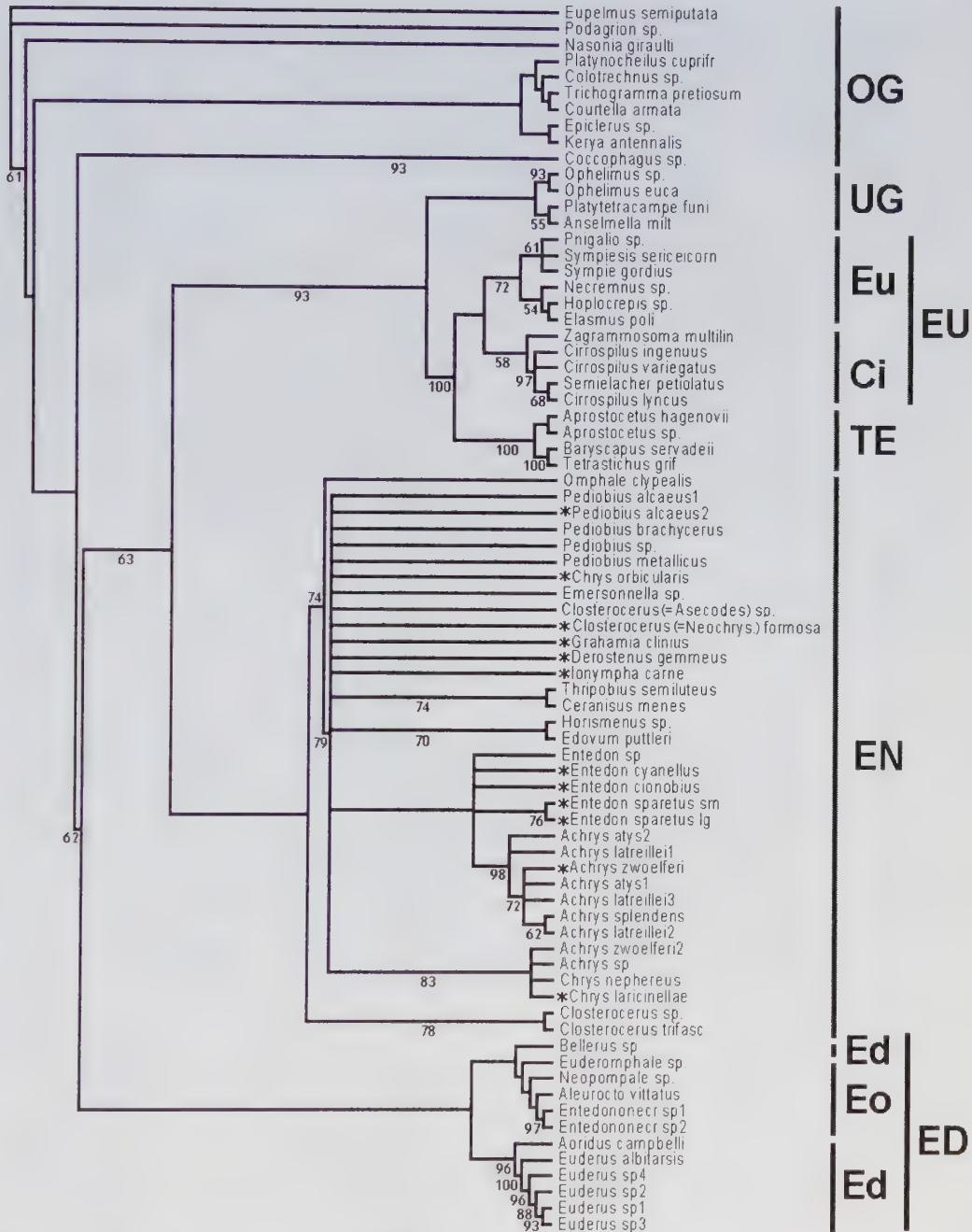


Figure 8 USC, strict consensus of 1818 trees obtained from the unlimited search for optimum trees by swapping branches using TBR algorithm and storing a maximum number of equally parsimonious trees in memory; see text for the abbreviations used

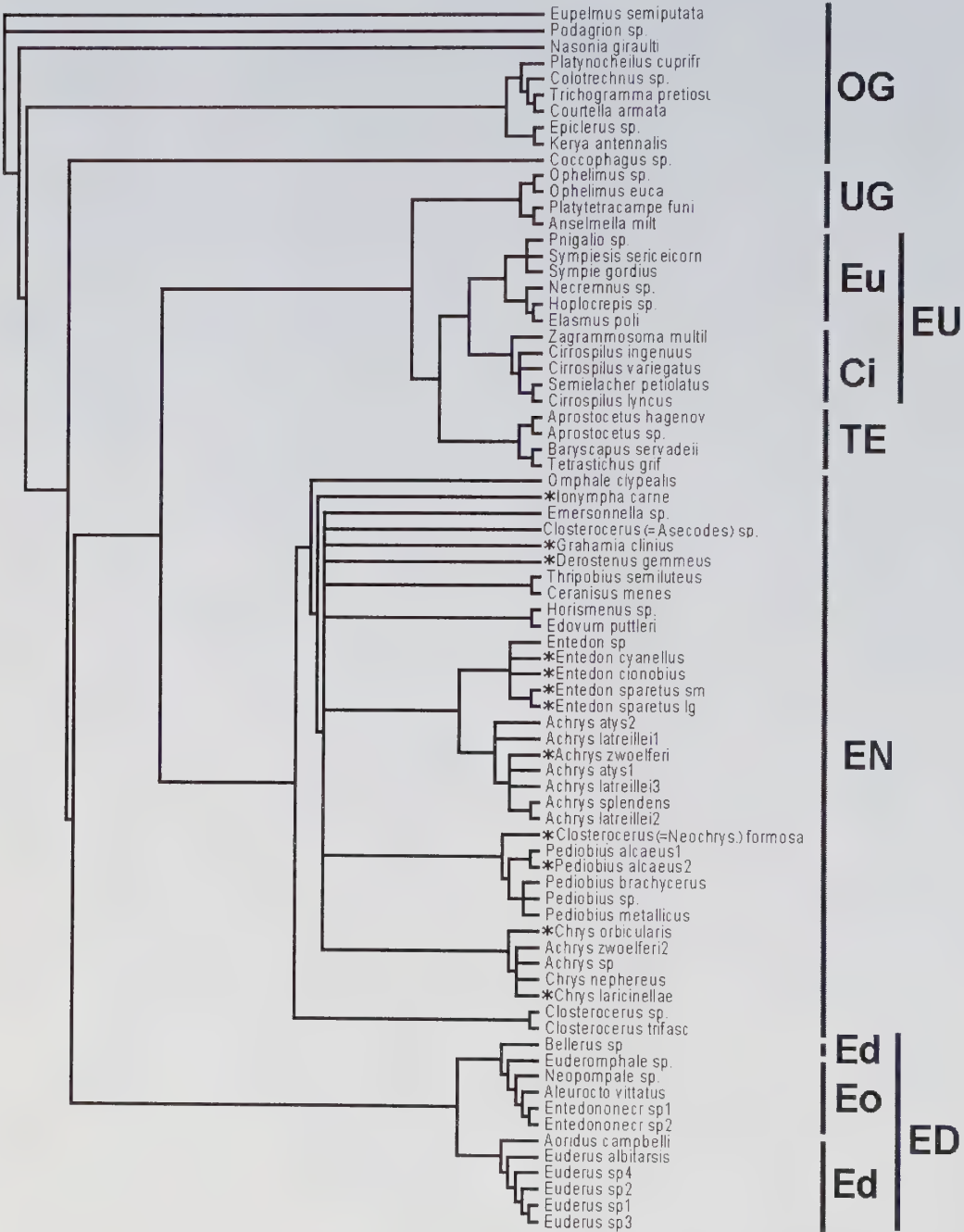


Figure 9 LSC, strict consensus of 100 trees obtained from the search for optimum trees by swapping branches using TBR algorithm and storing at most 100 equally parsimonious trees in memory (MAXTREES = 100)

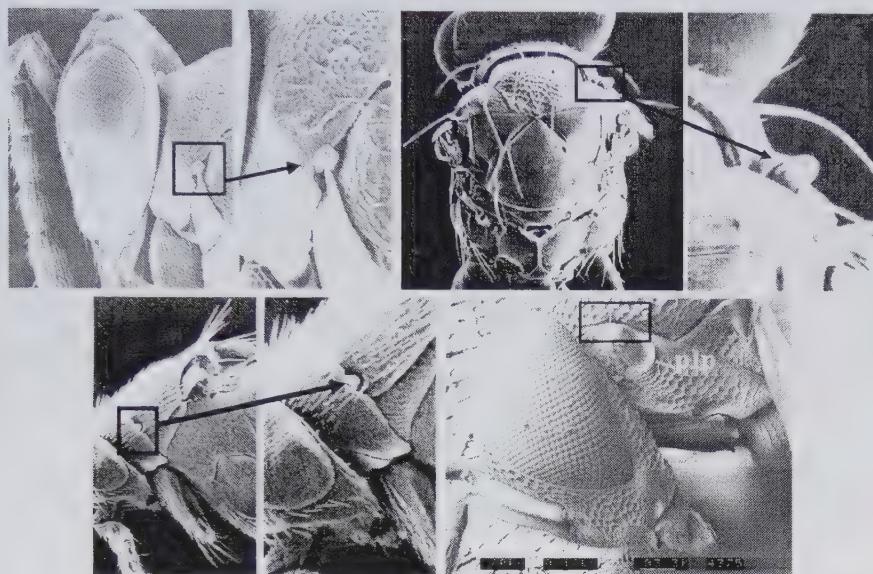


Figure 10 The first mesosomal spiracle (framed) of Eulophidae (a-c, SEM photos by LaSalle, J.; d, original): a, Tetrastichinae: *Aprostocetus granulatus* Ashmead; b, Eulophinae, Euplectrini: *Euplectrus* sp.; c, Eulophinae, Elasmini: *Elasmus* sp.; d, Entedoninae, *Entedon* sp.; plp, pronotal lateral plica

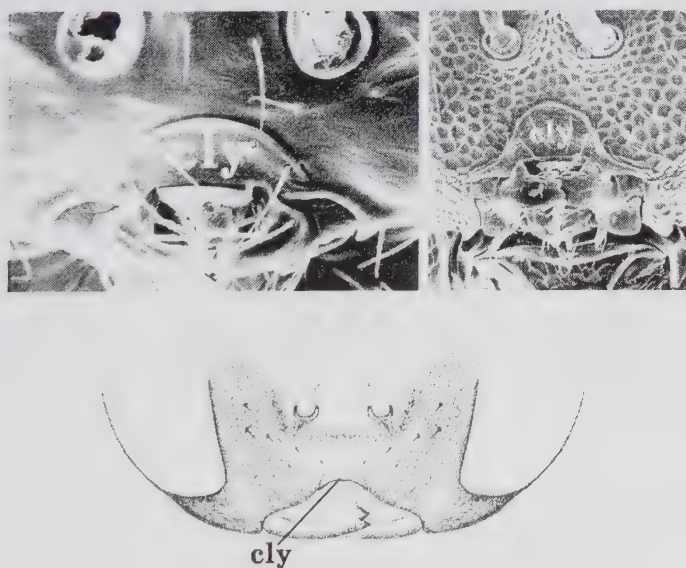


Figure 11 The shape of the clypeus and mandibles in Euderomphalini (a, b: SEM photos by LaSalle, J.) and Euderini (c, original): a, *Euderomphale* sp.; b, *Entedononecremnus* sp.; c, *Euderus* sp.; cly, clypeus

There was no molecular support for the monophyly of the entire subfamily in Gauthier *et al.* 2000. However, our alignment (combined of CLUSTAL W analysis and manual corrections) and PAUP* analysis have shown the entire subfamily to be monophyletic, however, without high bootstrap support. Euderomphalini and Euderinae represent one branch (see below), while Anselmellini + Ophelimini + Tetracampini and Tetrastichinae + Eulophinae compose another branch. The close relationship between Tetrastichinae and Eulophinae agrees with morphological data (e.g. the structure of the first mesosomal spiracles).

Anselmella, *Ophelimus* and *Platytetracampe*, being regarded as “unplaced groups” in Gauthier *et al.* 2000, have been found to be a part of Eulophidae, a sister group for Eulophinae + Tetrastichinae (with bootstrap of 93, Fig. 8). This largely corresponds to the partitioning of Eulophidae proposed by Bouček (1988, except for *Platytetracampe* treated there as an entedonine genus), despite such a structure of Eulophidae was regarded as doubtful by Gauthier *et al.* (2000). The structure of first mesosomal spiracle is not clear enough within this group, but it looks different from the condition observed in Entedoninae. Anyway, the whole Anselmellini, Ophelimini and Platytetracampini are easily separable from Entedoninae by greater number of antennal segments and by many other characters (Bouček 1988; Gauthier *et al.* 2000).

Recognition of the group

We propose to recognize entedonines among other eulophids by the possession of the hidden first mesosomal spiracle and additionally simultaneous presence of at least four of the following five characters:

1. Mesoscutum with 2 pairs of setae.
2. Face with frontal sulcus placed distantly from median ocellus.
3. Male scape with sensory pores restricted to ventral edge of scape.
4. Female gaster with 7 terga.
5. Submarginal vein with a break (slide) in the place of transition of the subcosta into the parastigma.

Characteristic features (occurring in most, but not all, or also in other Eulophidae or/and Chalcidoidea) generally are peculiar to 60-80% of Entedoninae: subcosta of submarginal vein often with 2 dorsal setae, mesoscutal midlobe with 2 pairs of setae, propodeum with a subspiracular tubercle and adspiracular groove, propodeal spiracle fully encircled. Characters of venation often used for recognition of Holarctic entedonines (long marginal vein, short stigmal and postmarginal veins, Schauff 1991; Gauthier *et al.* 2000) are poorly indicative for the group on the worldwide scale.

Euderomphalini

The tribe Euderomphalini proved to be monophyletic in the consensus trees (Table 1), although without significant bootstrap support. There were no new sequences of Euderomphalini compared with Gauthier *et al.* 2000, and their internal pattern of relationships corresponds in general to the data previously published, e.g. monophyly of the tribe persisted. However, the tribe proved to share a branch with euderines, what makes the placement of this group rather different in comparison with data published by Gauthier *et al.* 2000.

Table 2 Characters of Euderomphalini with respective arguments against their use in the diagnosis of the tribe (if regarded as part of Entedoninae and compared to the rest of them)

Character	Argument
1. Pronotum reduced	1. ... in many other Entedoninae, too
2. Scutellum overhanging dorsellum	2. ... in many other Entedoninae, too
3. Male scape with ventral groove present in apical half	3. ... row of sensory pores restricted apically in some other entedonines
4. Clypeus delimited dorsally	4. ... in many other Entedoninae, too
5. Antennal flagellum reduced, with 2 or 1 segment	5. ... in many other Entedoninae, too, e.g. <i>Closterocerus</i> , <i>Ceraninus</i>
6. Axilla, when indicated, generally placed entirely anteriorly to scuto-scutellar suture	6. ... in part of Euderomphalini axilla is entirely reduced, but in <i>Entedononecremnus</i> it is normal
7. Hosts are whiteflies	7. ... some other eulophids, as well (for instance, <i>Platytetracampe</i>)

LaSalle & Schauff (1994) proposed the following composition of Euderomphalini: *Euderomphale* group (*Baeoentedon*, *Euderomphale*, *Neopomphale*, *Pomphale*) and *Entedononecremnus* group (*Aleuroctonus*, *Dasyomphale*, *Entedononecremnus*). Members of the tribe are easily recognizable by their habitus (following LaSalle & Schauff 1994, Table 2).

The genus *Sporrongia* Gumovsky (1998) was described from Tobago Island, and has several characters shared with Euderomphalini (e.g. the pronotum reduced, scutellum overhanging the dorsellum, antennal flagellum reduced, with 1 segment only). However, the genus could not be placed within the tribe, probably rendering Euderomphalini paraphyletic.

From the morphological point of view the tribe Euderomphalini proved to be monophyletic in having rather specific clypeus (delimited as a convex plate with incised anterior margin) and mandibles (with massive base and semi-circularly bent cutting margin, Figs 11a, 11b).

These characters have never been considered despite the phylogeny of Euderomphalini was precisely discussed earlier (LaSalle & Schauff 1994; LaSalle 1999; LaSalle & Polaszek 2000). The specific shape of the clypeus in Euderomphalini resembles that of Cyclostome Braconidae (Goulet & Huber 1993). All known euderomphalines share these characters to some extent. The mandibles are not so clearly visible, but their general shape (with massive bases and bent cutting margins) is constant within the group.

I think the shape of the clypeus and mandibles are the best characters to define euderomphalines and to support their monophyly. The genus *Sporrongia* does not possess this peculiar shape of the clypeus and mandibles, what rules the genus out of Euderomphalini.

Euderomphalini and Euderini

The tribe Euderomphalini + *Bellerus* (Euderinae) has been found to be a sister group to euderine genera *Euderus* and *Aoridus*. They together represent a monophyletic unit in the trees obtained (Figs 8, 9, Table 1).

It is interesting that all studied representatives of Euderinae also have above-mentioned shape of the anterior clypeal margin (Fig. 11). Also the clypeus is always delimited in euderines, although this delimitation is generally formed by weak depressions (clypeus represents a concave plate in

Euderomphalinae). Such shape of the clypeus never appeared in the diagnoses of Euderinae. Taking into account that this character is rare (if not unique) within Chalcidoidea, there are certain reasons to suspect that Euderomphalini are more related with Euderinae than with Entedoninae.

All the studied Euderinae have first mesosomal spiracles exposed (although they are rather small). Current separation of Euderinae is based on the possession of 8 gastral terga (7 in the rest of Eulophidae). Other characters mentioned in their diagnoses (mesoscutum with notauli complete, scutellum with 2-3 pairs of sublateral setae, forewing venation etc.) work poorly for the entire subfamily (Bouček 1963, 1988; Coote 1994).

Most Euderomphalini possess the exposed protruding first mesosomal spiracles, although they are not easily observable because of the minute size of these wasps. The anterior margin of the lateral pronotal panel is not emarginated near this spiracle in euderomphalines, possibly due to rather reduced pronotum in this group.

Eventually, study on the morphology of *Euderomphale* persuaded me to propose a redefinition of its most distinct diagnostic character, e.g. the “large advanced axilla, being separated from the mesoscutum by a distinct suture” mentioned by most students of this genus. It was found that such an “axilla” represents rather side lobe of mesoscutum delimited by the remnant or modification of the notaulus. This character is peculiar to *Euderomphale* only, while in most representatives of Euderomphalini the axillae are significantly reduced (apart from *Entedononecremnus*, which has the axillae of normal size and shape). I consider that true axilla is totally reduced in *Euderomphale*, as well as in representatives of so-called genus complex. This redefinition makes some credits to the relationships with Euderinae, where the notauli are often well developed.

Another character indicating probable relationships between Euderomphalini and Euderini is the number of mesoscutal setae and of subcostal setae (the setae placed on the subcosta of the submarginal vein). Euderinae have more than 2 setae on both subcosta and mesoscutum (generally 4–6 setae). The species of only 4 genera of Euderomphalini have 2 (or occasionally 1) setae on the subcosta and species of only 3 of 7 genera have 2 setae on the mesoscutum (*Pomphale*, *Neopomphale*, *Baeoentedon*). Species of the rest genera have more than 2 setae at mentioned body parts. However, certain entedonines possess more than the two groundplan subcostal and mesoscutal setae, as well (see Gumovsky 1999; Ubaidillah *et al.* 2000).

Resuming the mentioned above discussion, I conclude that the new morphological characters not only help in the definition of established eulophid groups, but also indicate close relationships between Euderinae and Euderomphalini. So, I propose to regard the eulophid subfamily Euderinae Erdős, 1956 as consisting of two tribes: Euderini Erdős, 1956 and Euderomphalini Schafee, Rizvi, Khan, 1988. Both tribes are easily distinguishable from each other (Bouček 1963, 1988; Coote 1994; LaSalle & Schauff 1994), but the best character supporting monophyly of Euderini is a separation between eighth and ninth gastral terga, and Euderomphalini are monophyletic in having characteristic shape of mandibles, reduced metanotal dorsellum, considerably reduced pronotum, and peculiar host association (Aleyrodidae) as an indirect support of their monophyly.

Groups within Entedoninae

Entedon and *Achrysocharoides*

All species of *Entedon* + most of *Achrysocharoides* (except for two species, see below) form a monophyletic branch in USC and LSC, Table 1), although without strong bootstrap support.

Most species of the genus *Achrysocharoides* represent a monophyletic node in both USC and LSC (bases are the same for both trees, but sites 140 and 488 are not recorded for LSC, Table 1) having high bootstrap support. However, species of *Entedon* share two bases only, which support monophyly of the genus in LSC only (Table 1).

Both *Achrysocharoides* and *Entedon*, share a unique character, the pronotal lateral plica (Fig. 10d, plp). This character has never been reported earlier, although it proved to be stable within the group. Shape of the plica is somewhat different in the two genera, but both plicae are likely homological. The genera of *Pleurotropopsis*-complex also have this plica; however, it is longer and looks more like a transverse carina. There were no suitable samples of any representatives of the *Pleurotropopsis*-complex for the molecular studies to prove this proposition.

Achrysocharoides and *Entedon* are easily distinguishable by the shape of the frontal sulcus (transverse in *Achrysocharoides* and angulate or missing in *Entedon*), and the lateral pronotal callus (present in *Entedon* and absent in *Achrysocharoides*). Their relationships were not established earlier, but both molecular and morphological data make such an idea worth for consideration.

Ceraninus genus-complex

Two representatives of *Ceraninus* genus-complex (genera *Ceraninus* and *Thripobius*, both are parasitoids on thrips) are closely related in the obtained trees and this assemblage has high bootstrap support (74).

The association of these genera was not stable in Gauthier *et al.* (2000), and the genera fell outside of Entedoninae in some trees. The morphological background for such grouping is based on the following characters: vertexal suture stretching behind posterior ocellus, mandibles reduced (without any teeth), and temples wide.

Monophyly of this group (*Ceraninus*, *Goetheana*, *Thripobius*, *Entedonastichus*) is quite reliable, the thrips-parasitizing genera are traditionally treated as a monophyletic unit (Bouček 1977; Schauff 1991). More problematic is the internal subdivision of this complex into genera. The subdivision proposed by Bouček (1977) and accepted in general by Schauff (1991) was based mainly on characters varying in other genera, e.g., number of antennal segments, length of metasomal petiole. It is still possible that the species of thrips-parasitizing entedonine genera represent one and the same genus including some species groups, indeed.

Horismenus and *Edovum*

Genera *Horismenus* and *Edovum* were monophyletic in both trees obtained (Figs 8, 9, Table 1), and their association is of high bootstrap support (70). Both genera are closely related as it was pointed out by Schauff (1991). The genus *Horismenus* Walker contains over 50 species with wide spectrum of parasitoid-host relationships. The genus *Edovum* Grissell is monotypic, with the only species, *E. puttleri* Grissell. The latter is an egg parasitoid of coccinellid and chrysomelid beetles, the Colorado Potato Beetle *Leptinotarsa decemlineata* (Say), in particular.

Grissell (1980) pointed out that the genus is characterized by the combination of epicnemial carina, acetabular carina and a forked metasternal keel between the hindcoxae. These characters were found either gradual, or present in other genera as well, so that Schauff (1991) limited the diagnostic characters for *Edovum*. The most reliable difference between *Horismenus* and *Edovum* is the presence of the submedian propodeal grooves and the epicnemial carina (following Schauff

1991). Epinemial carina is a gradual character, present to some extent in *Entedon*, *Paracrias*, *Horismenus* and some other “hard-bodied” entedonines. The lateral grooves aside of the median stripe (= “tooth”) are disappearing in many smaller representatives of some other entedonine genera.

Otherwise, the anterior propodeal foveae (not mentioned earlier), the median propodeal stripe and mesosternal tooth interrupting the prepectus, make significant background for synonymy of *Horismenus* and *Edovum*.

Pediobius

There were no monophyly established for the genus *Pediobius* in USC, but in LSC it was monophyletic (Fig. 9, Table 1). It is remarkable that *Pediobius alcaeus* are separated from the rest sequenced species of the genus *Pediobius* in LSC based on the possession of thymine in 478 site (Table 1, Appendix 2). Small number of the bases shared by the species of the same genus is a reason for the weak support for a monophyly of the genus in USC, as is also the case with the genus *Entedon*. Monophyly of the genus *Pediobius* is not well supported. However, a complex of related genera (*Pediobius* Walker, *Rhynchentedon* Girault, *Pediobomyia* Girault, *Myrmocata* Bouček) is evidently monophyletic in having wide and robust propleural flange, sharply toothed lateral metapleural callus and propodeal submedian foveae (Gumovsky, 2001b). The placement of species of the genus *Pediobius* within this complex requires further investigations.

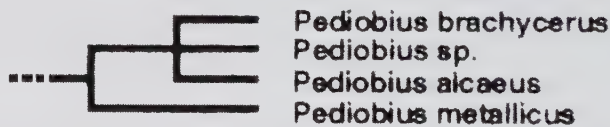


Figure 12 Fragment of one of the trees presented by Gauthier *et al.* (2000)

Upon examination of the tree by Gauthier *et al.* 2000, one can see that *P. metallicus* is removed from the rest of the genus (Fig. 12). However, our data have shown that this placement is rather unnatural. I have checked both AJ274485 and AJ274486 sequences (*P. metallicus* and *P. alcaeus*, respectively) from the EMBL/GenBank, and compared AJ274486 with my sequence of *P. alcaeus* (AJ306204). AJ274486 and AJ306204 are different in one base only (guanine instead of thymine in position 386), so it is evident that they represent one and the same species. *P. alcaeus*, in all likelihood, was erroneously named “*P. metallicus*” after decoding of intermediate abbreviations used in the preparatory molecular work. It is more probable, in view of the fact that *P. metallicus* has been known as *P. acantha* for a long time, that the abbreviation of the species names might be similar, and that has caused such a misinterpretation. Again, this error was evidently perpetuated in the trees proposed by Gauthier *et al.* 2000.

The morphological distinctness of the “*alcaeus* group” of *Pediobius* is based on the presence of the median propodeal tooth. This tooth is quite clearly visible in all the representatives of the group. Bouček (1965) mentioned that this structure is a derivation from the submedian carinae present in most *Pediobius* species. This is really possible, but the congruence between the molecular and morphological data persuades me to consider a special status of the “*alcaeus* group” of *Pediobius*, probably of separate generic or subgeneric level, in the future. Unfortunately, there

were no samples of the representatives of other genera of the *Pediobius*-complex being suitable for molecular studies, to verify placement of *P. alcaeus* within the genus-complex.

Ambiguous nodes and rest of genera

Two *Achrysocharoides* species form a node with two *Chrysocharis* species. This assemblage (having high bootstrap estimate, 83) is still unresolved and, despite two new species were added (*Achrysocharoides zweelferi* and *Chrysocharis larinellae*), it repeats one of the nodes in the trees of Gauthier *et al.* (2000). This grouping requires a more critical treatment; maybe it was caused by a contamination of the two samples of *Achrysocharoides* by a *Chrysocharis* DNA.

Two sequenced species of the genus *Closterocerus* fell out of the rest of Entedoninae (bootstrap support of 78). This generally corresponds to the pattern shown by Gauthier *et al.* (2000). There is no morphological support for such a placement from morphological viewpoint. Species of the genus *Closterocerus* (= *Asecodes*, *Neochrysocharis*, Gumovsky 2001a) possess the subtorular grooves, which bear an evidence of their monophyly. Further studies will show whether such a placement is caused by the limitations of the D2 region of the 28S rDNA gene, or this is a subject of contamination, or this is a certain signal for phylogenetic considerations. Gumovsky (2001a) synonymized *Asecodes* and *Neochrysocharis* with *Closterocerus*, however, there was no support for such a synonymy from the molecular data analysis, so far.

Omphale clypealis solely branched off from the Entedoninae except *Closterocerus*. The genus *Omphale* is easily recognizable (Hansson 1996, 1997) and likely stands separately from all the sequenced entedonines, so such a placement is well expected.

Emersonella sp., *Closterocerus* (= *Asecodes*) sp., *Closterocerus* (= *Neochrysocharis*) *formosa*, *Grahamia clinius*, *Derostenus gemmeus*, and *Ionympha carne* form a "brush" in the root of their node. *Closterocerus formosa* is a sister taxon for *Pediobius* in LSC, however, there are no morphological signals for such relationships.

Conclusions

The computer-assisted cladistic analysis of 66 representatives of Eulophidae and 10 outgroup taxa demonstrated monophyly of both Eulophidae as a whole and Entedoninae in particular. From the morphological point of view, Entedoninae have been found to be monophyletic in having first pair of the mesosomal spiracles hidden, which distinguishes them from other representatives of Eulophidae having these spiracles exposed and the pronotum being often emarginated around the spiracles.

The representatives of the tribe Euderomphalini have been found linked with members of eulophid subfamily Euderinae. Morphologically, euderomphalines are monophyletic in having convex delimited clypeus and specific mandibles of robust triangular shape. Euderomphalini and Euderinae share mentioned above clypeal structure, but differ in the number of the gastral terga (8 in Euderinae and 7 in Euderomphalini), shape of the pronotum (elongate in Euderini, rather reduced in Euderomphalini) and in the shape of mandibles (robust elongate in Euderinae). In regard of molecular and morphological similarity, the tribe Euderomphalini Schafee, Rizvi, Khan, 1988 is transferred to the subfamily Euderinae with the rest of Euderinae re-united to the tribe Euderini Erdős, 1956.

Genera *Achrysocharoides* and *Entedon* are related according to molecular data, and also in having semicircular plica in upper part of the lateral pronotal panel. The genera of *Pleurotroppopsis*-complex are possible related group for *Achrysocharoides* + *Entedon*, but their plicae are of somewhat different structure.

Genera *Horismenus* + *Edovum* and the genera of *Ceranisus* + *Thripobius* are closely related (based on molecular data), and are hardly separable morphologically. *Horismenus* + *Edovum* share the structure of lateral mesosoma and propodeal pattern, and *Ceranisus* + *Thripobius* share the shape of the vertexal suture.

Both molecular and morphological data show separateness of *Pediobius alcaeus* from the rest of *Pediobius*. This may be an initial background for further reassessment of its placement in Entedoninae.

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Appendix 1 Taxa included in analysis.

Species	Source / GenBank accession numbers of newly sequenced species
O U T G R O U P S	
EUPELMIDAE	
<i>Eupelmus semiputatus</i> (Girault)	EMBL
TORYMIDAE	
<i>Podagrion</i> sp.	EMBL
PTEROMALIDAE	
<i>Nasonia giraulti</i> Darling	EMBL
<i>Colotrechus</i> sp.	EMBL
TRICHOGRAMMATIDAE	
<i>Trichogramma pretiosum</i> Riley	EMBL
APHELINIDAE	
<i>Epiclerus</i> sp.	EMBL
APHELINIDAE	
<i>Platynocheilus cuprifrons</i> (Nees)	EMBL
AGAONIDAE	
<i>Courtella armata</i> (Wiebes)	EMBL
UNPLACED, Keryini	
<i>Kerya antennalis</i> Bouček	EMBL
E U L O P H I D A E	
Ophelimini	
<i>Ophelimus</i> sp.	EMBL
<i>Ophelimus eucalypti</i> (Gahan)	EMBL
Platytracampini	
<i>Platytracampe funiculus</i> Girault	EMBL
Anselmelini	
<i>Anselmella miltoni</i> Girault	EMBL
EUDERINAE	
Euderini	
<i>Bellerus</i> sp.	EMBL
<i>Euderus albitarsis</i> (Zetterstedt)	EMBL
<i>Euderus</i> sp. (1)	EMBL
<i>Euderus</i> sp. (2)	EMBL
<i>Euderus</i> sp. (3)	EMBL
<i>Euderus</i> sp. (4)	EMBL
<i>Aoridus campbelli</i> Yoshimoto	EMBL
Euderomphalini	
<i>Euderomphale</i> sp.	EMBL
<i>Aleuroctonus vittatus</i> (Dozier)	EMBL
<i>Neopompale</i> sp.	EMBL
<i>Entedononecremnus</i> sp. (1)	EMBL

Species	Source / GenBank accession numbers of newly sequenced species
<i>Entedononecremnus</i> sp. (2)	EMBL
EULOPHINAE	
Eulophini	
<i>Pnigalio</i> sp.	EMBL
<i>Hoplocrepis</i> sp.	EMBL
<i>Sympiesis sericeicornis</i> (Nees)	EMBL
<i>Sympiesis gordius</i> (Walker)	EMBL
<i>Necremnus</i> sp.	EMBL
Elasmini	
<i>Elasmus polistis</i> Burks	EMBL
Cirrospilini	
<i>Semielacher petiolatus</i> (Girault)	EMBL
<i>Zagrammosoma multilineatum</i> (Ashmead)	EMBL
<i>Cirrospilus lyncus</i> Walker	EMBL
<i>Cirrospilus ingenuus</i> Gahan	EMBL
<i>Cirrospilus variegatus</i> (Masi)	EMBL
TETRASTICHINAE	
<i>Aprostocetus hagenovii</i> (Ratzeburg)	EMBL
<i>Baryscapus servadeii</i> (Domenichini)	EMBL
<i>Tetrastichus giffardianus</i> Silvestri	EMBL
<i>Aprostocetus</i> sp.	EMBL
ENTEDONINAE	
<i>Achrysocharoides atys</i> (Walker) (1)	EMBL
<i>Achrysocharoides atys</i> (Walker) (2)	EMBL
<i>Achrysocharoides latreillei</i> (Curtis) (1)	EMBL
<i>Achrysocharoides latreillei</i> (Curtis) (2)	EMBL
<i>Achrysocharoides latreillei</i> (Curtis) (3)	EMBL
<i>Achrysocharoides splendens</i> (Delucchi)	EMBL
<i>Achrysocharoides zwoelferi</i> (Delucchi) (1)	United Kingdom, England, a/n AJ306201
<i>Achrysocharoides zwoelferi</i> (Delucchi) (2)	EMBL
<i>Achrysocharoides</i> sp.	EMBL
<i>Closterocerus</i> (=Asecodes) sp.	EMBL
<i>Ceraninus menes</i> (Walker)	EMBL
<i>Chrysocharis larinellae</i> (Ratz.)	United Kingdom, England, a/n AJ306209
<i>Chrysocharis nephereus</i> (Walker)	EMBL
<i>Chrysocharis orbicularis</i> (Nees)	United Kingdom, England, a/n AJ306202
<i>Closterocerus</i> sp.	EMBL
<i>Closterocerus trifasciatus</i> Westwood	EMBL
<i>Derostenus gemmeus</i> (Walker)	United Kingdom, England, a/n AJ306208
<i>Edovum puttleri</i> Grissell	EMBL
<i>Emersonnella</i> sp.	EMBL
<i>Entedon cionobius</i> Thomson	Bulgaria, Rhodopi Mountains, a/n AJ306200

Species	Source / GenBank accession numbers of newly sequenced species
<i>Entedon cyanellus</i> Dalman	Bulgaria, Rhodopi Mountains, a/n AJ306197
<i>Entedon</i> sp.	EMBL
<i>Entedon sparetus</i> Walker, large variety	Bulgaria, Rhodopi Mountains, a/n AJ306199
<i>Entedon sparetus</i> Walker, small variety	Bulgaria, Rhodopi Mountains, a/n AJ306198
<i>Grahamia clinius</i> (Walker)	United Kingdom, England, a/n AJ306207
<i>Horismenus</i> sp.	EMBL
<i>Ionympha carne</i> (Walker)	United Kingdom, England, a/n AJ306206
<i>Closterocerus</i> (= <i>Neochrysocharis</i>) <i>formosa</i> (Walker)	United Kingdom, England, a/n AJ306205
<i>Omphale clypealis</i> Thomson	EMBL
<i>Pediobius alcaeus</i> Walker (1)	EMBL
<i>Pediobius alcaeus</i> Walker (2)	United Kingdom, England, a/n AJ306204
<i>Pediobius brachycerus</i> Thomson	EMBL
<i>Pediobius metallicus</i> (Nees)	EMBL
<i>Pediobius</i> sp.	EMBL
<i>Thripobius semiluteus</i> Bouček	EMBL

Appendix 2: see on CD enclosed

MOLECULAR INSIGHTS TO FIG WASP TAXONOMY AND BIOLOGY (CHALCIDOIDEA: AGAONIDAE)

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Key words: Fig wasp, Agaonidae, Chalcidoidea, *Ficus*, molecular marker, phylogeny, coevolution

Introduction

In recent years, molecular markers that exploit natural variation in DNA sequences have undergone rapid development and impacted upon many areas of biology. While the most obvious applications are in fields like genetics and cell biology, they have also proved to be valuable tools for ecology, evolutionary biology and taxonomy. To date, fig wasp molecular markers have been used exclusively for phylogenetic studies, aiming to clarify issues concerning fig wasp classification, evolution and coevolution. The first few molecular phylogeny studies have yielded several novel insights to fig wasp biology, which I discuss in this brief review, as well as suggesting promising avenues for future work.

Results and Discussion

Fig wasp taxonomy and biology

The term “fig wasps” is often used to refer to all parasitic Hymenoptera that develop in the syconia (fig inflorescences) of fig trees (*Ficus* species). While this ecological categorisation is useful for many purposes, notably ecological and behavioural studies, it can mask the fact that fig wasps are taxonomically diverse and include several different lineages with diverse biological attributes. The vast majority of all fig wasps belong to the superfamily Chalcidoidea, although there are a few species from the superfamily Ichneumonoidea (family Braconidae). Amongst the chalcidoid fig wasps, a few taxa can be placed clearly into families (Ormyridae, Eurytomidae, Pteromalidae, Torymidae) that contain many genera not associated with figs. However, the vast majority of all fig wasp genera and species have been classified in six subfamilies of wasps (Agaoninae, Epichrysomallinae, Sycoecinae, Sycophaginae, Sycoryctinae, Otitesellinae) associated exclusively with *Ficus* syconia. Many of the genera are well-defined and the females can be identified readily using the key provided by Bouček (1988). However, the phylogenetic relationships of the subfamilies are controversial and less stable. For example, the subfamily Epichrysomallinae has been placed variously in families Torymidae, Pteromalidae (Bouček *et al.* 1981) and Agaonidae (Bouček 1988) but is currently unplaced (Rasplus *et al.* 1998). Bouček (1988) found no convincing basis to place any of the six fig wasp subfamilies in other families and included them all in a single family Agaonidae with all members fig-associated. In his scheme the fig-pollinating wasps were a subfamily (Agaoninae) of the more inclusive family Agaonidae.



Wasps that inhabit fig syconia show many morphological adaptations to this unusual niche and this creates two problems: first, adaptations like unusual head shapes, long ovipositors and male aptery may evolve convergently in different lineages (van Noort & Compton 1996) and, second, morphology may be so derived that it is difficult to identify outgroups amongst chalcid taxa that do not inhabit figs. In addition, there is a general paucity of comprehensive morphological studies and specialists capable of the necessary analyses (Bouček 1993), and the situation is not helped by outstanding classificatory problems in the wider Chalcidoidea, where Pteromalidae is an acknowledged “dumping ground”, and where monophyly has yet to be demonstrated for many families (Campbell *et al.* 2000).

The best-known group of fig wasps, in terms of both taxonomy and biology, are the fig-pollinating wasps (Agaonidae). These are the only wasps that actually pollinate the figs, which they may do actively or passively (Kjellberg *et al.* 2001). In general, it appears that there is a one-to-one correspondence of agaonid and *Ficus* species and, since about 750 *Ficus* species are known (Berg 1989), there should be a similar number of agaonid species. The association between figs and agaonids is an obligate mutualism since neither partner can reproduce alone. Agaonids are the only vectors of fig pollen, while agaonid larvae develop only within galls in female flowers in fig syconia. Although it is an obligate relationship, there are also reproductive conflicts (Herre 1996). For example, each female flower can give rise to either a seed or a wasp. Selection on figs favours production of both (because wasps function as pollen vectors) but selection on wasps should favour maximisation of the number of wasp offspring.

While fig-pollinating wasps have received the most attention, non-pollinating fig wasps are far more diverse and speciose, with the majority of species still awaiting description (Cook & Lopez-Vaamonde 2001). Most fig species have just one pollinating wasp but may play host to as many as 30 different species of non-pollinating wasps. The majority of non-pollinating wasps are probably phytophagous but there are also species that areinquilines and others that are true parasitoids. While fig wasps have proved excellent models for numerous studies in behavioural ecology, the basic trophic ecology of most species, and consequent structure of communities, is essentially unknown.

Molecular phylogeny and the classification of fig-pollinating wasps

There have been several studies of fig wasp molecular phylogeny in recent years and these have mostly used DNA sequence data from one or more of four gene regions – mitochondrial cytochrome oxidase (COI, COII) and cytochrome b (Cytb), and the D1, D2 and D3 expansion regions of the nuclear 28S ribosomal DNA (28S) (Table 1).

Monophyly of all fig-pollinating wasps is supported by analyses of 15 of the 20 genera using COI (Machado *et al.* 2001) and of 10 genera using a longer COI/COII fragment (Weiblen 2001), although these and earlier studies (Yokoyama 1995; Herre *et al.* 1996, Machado *et al.* 1996) included very few chalcidoids not associated with figs. Rasplus *et al.* (1998), who used a nuclear gene fragment (28s rDNA) and included a wider range of chalcidoid taxa, also found support for fig-pollinator monophyly. However, their study was focused on a different question (see below) and included only two pollinator genera. I am not aware that anyone has seriously questioned the monophyly of fig-pollinating wasps, but a really conclusive test should nevertheless include representatives of all 20 genera and a wide range of chalcidoid outgroups.

The sister taxon of the Agaonidae is unknown and difficult to establish because of the highly derived morphology of the pollinators. Consequently, molecular markers may provide the most expedient way to investigate the relationships of fig wasps to other chalcidoid families. Rasplus *et al.* (1998) found that Agaonidae was the sister group to all other Chalcidoidea, but relatively few other chalcid families were represented in their analysis. Subsequently, Campbell *et al.* (2000) made the first attempt at an inclusive molecular phylogeny of the Chalcidoidea, but did not include any fig-pollinating genera (a sycoecine and an otitiselline were analysed). The gene fragment used, the D2 region of 28S, shows a lot of variation between different agaonid genera, and even within one genus studied (*Pleistodontes* – Lopez-Vaamonde *et al.* 2001) and can provide considerable phylogenetic signal. However, much of the variation is due to insertions and deletions of nucleotides so alignment of DNA sequences may be difficult and it is important to establish the degree to which phylogenies are robust to different alignment methods or weighting schemes. 28S is a valuable marker, but resolution of family relationships will probably require the additional use of other markers. Good candidates would include 18S rDNA and protein-coding nuclear genes. In the latter category, long wave rhodopsin, which has been used recently with the Cynipoidea (Rokas *et al.* 2001), is a possibility worth exploring.

Table 1 Fig wasp molecular phylogenies (COI and COII refer to subunits I and II respectively of the cytochrome oxidase gene of mitochondrial DNA (mtDNA). CytB refers to the cytochrome b gene and 12S to the 12S ribosomal DNA, both in the mtDNA. Nuclear genes studied have been limited to parts of the 28S ribosomal DNA (28S) and internal transcribed spacer 2 (ITS2) of the ribosomal DNA cluster. The number of genera studied is indicated, as well as the number of species in parentheses)

Genes studied	Taxa studied	Reference
COI (not given)	Eight fig wasp genera (18 spp)	Yokoyama 1995
12S (350), COI/II (550)	Six pollinator genera (10 spp.)	Herre <i>et al.</i> 1996
12S (320), COII (684)	<i>Pegoscapus</i> / <i>Tetrapus</i> pollinators (8 spp.); <i>Idarnes</i> / <i>Critogaster</i> non-pollinators (9 spp.); 11 fig wasp genera	Machado <i>et al.</i> 1996
28S (719)	14 fig wasp genera (15 spp), 6 other chalcid genera	Rasplus <i>et al.</i> 1998
CytB (800)	14 <i>Ceratosolen</i> pollinator species	Kerdelhue <i>et al.</i> 1999
28S (700-1000), ITS2 (300-400), CytB (400)	15 <i>Pleistodontes</i> pollinator species; 15 <i>Sycoscapter</i> non-pollinator species	Lopez <i>et al.</i> 2001
COI (800)	15 pollinator genera (32 spp.)	Machado <i>et al.</i> 2001
COI-COII (1900)	Ten pollinator genera (43 spp.)	Weiblen 2001

Polyphyly of non-pollinating fig wasps: multiple invasions of the syconium

Rasplus *et al.* (1998) analysed relationships based on 28S for at least 2 genera from each of the 6 fig wasp subfamilies, along with representatives of the three chalcidoid families (Torymidae, Pteromalidae, Eurytomidae) that have been considered closely related to fig wasps. Their main



finding was that Agaonidae *sensu* Bouček (1988) is a polyphyletic assemblage of lineages, some of which are more closely related to other members of the “pteromaloid complex” that do not inhabit figs (Table 2). Specifically, members of Otitesellinae, Sycoryctinae and Sycoecinae were interspersed in the phylogenies with pteromalids not from figs and were therefore assigned to Pteromalidae. In addition, the other two subfamilies (Epichrysomallinae & Sycophaginae) did not cluster with either the pollinators or any other taxa, so currently remain unplaced at family level. In view of these results, the pollinator subfamily Agaoninae was raised to its previous rank of Agaonidae. Bouček (1988), in proposing a wider Agaonidae, had emphasised that most fig wasp genera share a postgenal bridge and lack an occipital carina. Such characters are unlikely to be strongly adaptive to life in a fig and could therefore be good indicators of phylogeny (Rasplus *et al.* 1998). However, after further studies of these head structures, Rasplus *et al.* (1998) concluded that there were three different groups of structures that were probably not homologous in origin. Furthermore, analysis of ovipositor structures also contradicts the validity of a wider Agaonidae (Quicke *et al.* 1994).

Table 2 Two recent views of fig wasp classification (descriptions of biology are generalizations)

Subfamily	Bouček (1988) Family	Rasplus (1998) Family	Biology
Agaoninae	Agaonidae	Agaonidae	Pollinators, enter figs to lay eggs, induce galls in female flowers
Epichrysomallinae	Agaonidae	unplaced	Non-pollinators, most lay eggs through wall, induce large galls.
Sycophaginae	Agaonidae	unplaced	Non-pollinators, most lay eggs through fig wall, gall inducers
Sycoecinae	Agaonidae	Pteromalidae	Non-pollinators that enter figs. Gall inducers
Otitesellinae	Agaonidae	Pteromalidae	Non-pollinators, most oviposit through fig wall. Gall inducers
Sycoryctinae	Agaonidae	Pteromalidae	Non-pollinators, oviposit through fig wall. Gall inducers, inquiline and parasitoids

The implication of this analysis is that there has been a great deal of convergent adaptive evolution. This applies to lifestyle, with several different lineages colonising figs at different times in evolutionary history; it applies to morphology, with adaptive characters like long ovipositors and male aptery arising repeatedly; and it also applies to behaviour, since the habit of entering the syconium in order to oviposit has arisen at least five different times (Rasplus *et al.* 1998). Several issues remain unresolved; for example it appears that Sycoryctinae and Otitesellinae may not be monophyletic groups. At least for Otitesellinae, this had been suggested before, based on morphology (Bouček 1993). Nevertheless, these molecular results are encouraging and molecular phylogeny should provide valuable further insights to these problems, as long as taxon sampling is appropriate.

Evolution and radiation of fig-pollinating wasps

The internal phylogeny of the Agaonidae is interesting for several reasons, mostly concerning adaptations to, and variation within the fig/pollinator mutualism. Recently, Machado *et al.* (2001) combined fossil and molecular data to try to estimate the age of the mutualism, which is certainly an evolutionary success, having given rise to over 750 described fig species distributed throughout the warmer regions of the world (Berg 1989). A fossil from Dominican amber, that is placed in the extant genus *Pegoscapus*, is at least 20 MYA (Poinar 1993), while an older Canadian specimen, suggested to belong to the basal genus *Tetrapus*, is dated at 34.5 MYA (Yoshimoto 1975; Machado *et al.* 2001). These dates come from geological evidence and the *Pegoscapus* fossil date was used to calibrate branch lengths on a maximum likelihood phylogeny of agaonid genera, yielding an estimate of 87.5 \pm 12.8 MYA for the origin of the mutualism. How does this molecular date compare with other dates from fossil evidence? The oldest fossil fig is 50 MYA (Collinson 1989), while the oldest chalcidoid fossils are about 90 MYA, and the oldest pteromalids and eurytomids about 60 MYA (Bouček 1988: 22). However, some of the chalcid fossils are already specialised (Bouček 1988: 22) and the Chalcidoidea may have radiated in the Cretaceous (Campbell *et al.* 2000) or even the late Jurassic (Yoshimoto 1975). In any case, fossils can only give estimates of the minimum age of a clade whereas molecular dating estimates the date of origin of the clade so molecular dates of origin should always exceed the oldest fossils. Since the accuracy of molecular branch length calibration depends in turn on the fossil reference points, it would be valuable to have multiple calibration points for the phylogeny. One approach to this would be to add to the molecular phylogeny further chalcid and hymenopteran taxa that have better fossil records than the fig wasps.

Interestingly, the calibrated molecular phylogeny of Machado *et al.* (2001) suggests that the radiation of pollinator genera is essentially concordant with the geological splitting of Gondwana. Molecular phylogenies have also given biogeographical insights in two other studies: *Ceratosolen* species pollinating figs of the subgenus *Sycomorus* fall into distinct African and Malagasy clades (Kerdelhue *et al.* 1999) and *Pleistodontes*, which is primitively a Papuan rainforest genus, includes a recent derived clade of species that pollinate lithophytic figs in the arid zone of western Australia (Lopez-Vaamonde *et al.* 2001).

Morphology and molecules

Wiebes (1982) made a preliminary phylogenetic study of the Agaonidae using morphological characters. His main conclusion was that the pollinators split into two subfamilies – Blastophaginae (mandibular appendages with lamellae, short antennal scapes) and Agaoninae (mandibular appendages with teeth, long antennal scapes). A difficulty with this interpretation was that the genus *Pleistodontes* contains some species with lamellae and others with teeth on the mandibular appendages (Lopez-Vaamonde *et al.*, *in press*). This could have resulted from problems with the identities of some *Pleistodontes* species; however, a recent revision of *Pleistodontes* has not changed this dilemma (Lopez-Vaamonde *et al.*, *in press*). Furthermore, molecular studies provide consistent strong support for the monophyly of *Pleistodontes* and contradict the validity of Agaoninae and Blastophaginae (Lopez-Vaamonde *et al.* 2001, Machado *et al.* 2001; Weiblen 2001). Consequently, it now seems most likely that Agaoninae and Blastophaginae are not valid subfamilies of pollinating wasps.

Comparing morphological and molecular evolution can be interesting and revealing in itself. For example, Lopez-Vaamonde *et al.* (2001) found that DNA sequence divergence between pairs of pollinating *Pleistodontes* was similar to that between pairs of non-pollinating *Sycoscapter* species from the same fig species. In contrast, while females of *Pleistodontes* species show considerable morphological diversity, females of *Sycoscapter* species differed little, apart from in overall size and relative ovipositor length. This may reflect the fact that much greater morphological evolution is demanded by the need to enter the syconium than by the need oviposit through it from the outside (Lopez-Vaamonde *et al.* 2001).

Many morphological characters of pollinators may be subject to convergent selection, making them poor indicators of phylogeny. Nevertheless, it is informative to compare morphological and molecular data sets and Weiblen (2001) has argued that, while head characters may be highly convergent, other morphological features show less homoplasy and may be more indicative of phylogeny.

Coevolution

Coevolution has two components, coadaptation and cospeciation, and both require rigorous testing. Coadaptation refers to the respective adaptive responses to the reciprocal selection pressures exerted by interacting species, and is believed to be important in fig-pollinator associations (Herre 1996; van Noort & Compton 1996). Cospeciation refers to the pattern of speciation of the two lineages, hypothesising that their cladogenetic patterns are identical and contemporaneous. Molecular phylogenies should be especially useful for estimating, and then comparing, phylogenies of figs and their pollinators. So far, nobody has published an in depth comparison of fig and wasp phylogenies, although limited preliminary studies (Yokoyama 1995; Herre *et al.* 1996) were consistent with substantial cospeciation. A less incisive but still valuable approach is to compare the molecular phylogeny of one group with the taxonomy of the other. Using this approach, both fig (Weiblen 2000) and pollinator (Machado *et al.* 2001; Weiblen 2001) phylogenies are consistent with a history of considerable cospeciation. To date, the development of molecular markers for fig phylogeny has been less successful than for wasp phylogeny, with only one paper published (Weiblen 2000). It is the lack of fig phylogenies that currently prevents cospeciation analyses at the species level.

It is also possible that some lineages of non-pollinating fig wasps may cospeciate with their fig hosts and/or the fig pollinators. A comparison of the molecular phylogenies of eight pairs of Panamanian pollinating (*Pegoscapus* & *Tetrapus*) and non-pollinating (*Idarnes* & *Critogaster*) wasps from the same fig species suggested that cospeciation might be common at this taxonomic level (Machado *et al.* 1996). More recently, a comparison of the phylogenies of 15 pairs of *Pleistodontes* pollinator species and associated *Sycoscapter* non-pollinator species showed significant congruence consistent with substantial, but far from complete, cospeciation of the two genera (Lopez-Vaamonde *et al.* 2001). Lopez-Vaamonde *et al.* (2001) argued that the partial match might be explained by shifts to new host fig species being somewhat constrained but still easier for fig wasp taxa that oviposit from outside, rather than inside, the syconium.

The phylogenies of genera of fig-pollinating wasps (and *Ficus* sections) also allow us to trace the evolution of key characters involved in the mutualism. Fig-pollinating wasps may be either active or passive pollinators and there is good evidence that figs invest more in pollen production when they have passive pollinators (Kjellberg *et al.* 2001). Wasp molecular phylogenies (Machado

et al. 1996, 2001; Weiblen 2001) suggest strongly that *Tetrapus*, a passive pollinator, is the most basal genus, and that active pollination evolved in the common ancestor of all the other genera. However, active pollination behaviour appears to have been lost secondarily in at least some members of several genera (Kjellberg *et al.* 2001; Machado *et al.* 2001).

About half of all fig species are monoecious, producing wasps and seeds from the same trees, while the other half are dioecious, producing wasps on male trees and seeds on female trees. Breeding system has been used as a taxonomic character to group together all dioecious figs, but this is now being questioned by molecular phylogenies of both figs (Weiblen 2000) and pollinators (Machado *et al.* 2001; Weiblen 2001). It appears that the pollinators of dioecious figs do not form a monophyletic group and that there have been multiple changes in breeding system.

The one-to-one correspondence of fig and pollinator species is quoted widely. However, it has not been subjected to substantive testing and may be an over-generalisation. Several biases probably prevent reports of exceptions. First, non-taxonomist biologists expecting one pollinator species are unlikely to look carefully for further species on the same fig. Second, not many fig species have had their pollinators sampled and identified repeatedly at different times and localities. Third, cryptic species may well exist, as in many other Hymenoptera Parasitica. Over the last few years we have sampled repeatedly the *Pleistodontes* pollinators of figs in the section *Malvanthera* in Australia. Three out of twelve well-sampled *Ficus* species have two distinct *Pleistodontes* pollinator species (Lopez-Vaamonde *et al.*, *in press*). These species are all morphologically distinct and relatively common within the host plant range (although one is found only in a restricted part of the host fig range). A comparable repeated sampling of (mostly African) figs in the section *Sycomorus* also reported 3/12 fig species with multiple pollinators (Kerdelhue *et al.* 1999). If 25% figs have more than one pollinator, is there a one-to-one rule? Perhaps it applies better in the other direction. It seems that, barring mistakes, most wasp species are reported from only one fig species. Interestingly, Kerdelhue *et al.* (1999) reported only one species found in two figs (*F. mucoso* and *F. sycomorus*) and this was the "cuckoo" species *Ceratosolen galili*, which enters figs but does not pollinate them.

Three cases of co-pollinators have been included in recent molecular phylogenies. *F. sur* is widespread in Africa and has three recorded pollinators. Molecular data support sister species status for the two west African species (*Ceratosolen silvestrianus* & *C. flabellatus*) and do not rule out that the third (eastern) species (*C. capensis*) is the sister group to the other two. In contrast, *F. sycomorus* and *F. mucoso* both have unique active pollinators but share the cuckoo pollinator *C. galili*. The phylogeny suggests that *C. galili* is only distantly related to the other two species, and it probably co-occurs with them following a host shift (Kerdelhue *et al.* 1999).

Conclusion

The first molecular phylogenies of fig wasps have added considerably to our understanding of the evolution of this group of insects and their interaction with fig plants. COI and 28S have proved the most informative gene regions to date but there is a need for development of further (nuclear) markers that are informative at the deeper phylogenetic levels. Some issues may well be soluble using existing markers but require better taxonomic sampling. For example, the monophyly of most genera is untested because studies to date have tended to represent most genera by only a few species. Similarly, placement of different fig wasp subfamilies in the wider frame of the Chalcidoidea requires denser and wider taxon sampling.



Molecular markers can also be used for many purposes other than phylogeny, but none of these have yet been applied in fig wasps. Useful approaches for future studies could include application of microsatellite and AFLP markers to estimate relatedness and parentage in behavioural ecology studies, and development of species-specific DNA probes or PCR assays for distinguishing between cryptic species, an approach now used widely for mosquito species complexes.

Finally, I would like to end with a telling case study based on the wide interest in the specificity of fig-pollinator associations. Wiebes (1979: 5) listed *F. obliqua* as one of a few fig species that appeared to host two different wasp species (*Pleistodontes imperialis* and *P. greenwoodi*) and thus to break the one-to-one rule. In retrospect, we can now say that he was wrong, and right. He was wrong because of a taxonomic inaccuracy on the botanical side. *P. greenwoodi* was listed as the pollinator of *F. obliqua* and *P. imperialis* as the pollinator of *F. obliqua* var. *petiolaris*. However, *P. imperialis* is the well-established and only pollinator of *F. rubiginosa* and detailed investigation of the Australian fig species using ordination analyses (Dixon *et al.* 2001) showed that there were only two taxa – *F. obliqua* (previously var. *obliqua*) and *F. rubiginosa* (including what was previously termed *F. obliqua* var. *petiolaris*). On the other hand, he was right, because of poor sampling. The “real” *F. obliqua* is a common and widespread tree in Eastern Australia and pollinator collections from most of the range consist of *P. greenwoodi*. However, four recent collections from North Queensland all contain only a different (and new) species, *P. xanthocephalus* (Lopez-Vaamonde *et al.*, *in press*), so *F. obliqua* does have two pollinator species. Furthermore, molecular analyses of *Pleistodontes* suggest that *P. xanthocephalus* and *P. greenwoodi* are sister species (Lopez-Vaamonde *et al.* 2001), which have probably diverged and speciated whilst in association with *F. obliqua*. There may yet be more to add to this story since *F. obliqua* may also occur outside Australia. However, it already serves to illustrate just how important good taxonomy and field sampling remain, and how they can be combined with new molecular data to unravel evolutionary patterns.

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PRELIMINARY MOLECULAR PHYLOGENETIC ANALYSIS OF CRYPTINAE AND RELATED TAXA BASED ON 28S D2+D3 rDNA ANALYSED USING POY (HYMENOPTERA: ICHNEUMONIDAE)

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Abstract – A preliminary cladistic analysis of the ichneumonid wasp subfamily Cryptinae based on 28S rDNA sequence data is presented. Trees were constructed using the programme POY which simultaneously finds homology lines within sequence data during tree searching rather than creating an alignment first and then analysing that. POY analyses were carried out using a range of gap:substitution cost ratios. All analyses recovered representative Ichneumoninae just within the Cryptinae, though it should be noted that only two outgroup taxa were included and rooting may therefore be unreliable. *Alomya* was never recovered with Ichneumoninae, but was placed rather basally in Cryptinae. Trees were broadly congruent with current major cryptine divisions based on morphology.

Key words: Ichneumonidae, Cryptinae, cladistics, molecular phylogeny

Introduction

The Cryptinae is an enormous subfamily of ichneumon wasps, comprising more than 380 recognised genera (Townes 1970; Yu & Horstmann 1997). Its taxonomy is, not surprisingly given its size, difficult, but this is exacerbated because many of the subtribes and at least one of the tribes are not defined by any particularly convincing characters (Gauld 1984). It is likely that many changes in classification will be required once a better understanding of relationships has been acquired.

The Cryptinae have for a long time been considered as being closely related to another very large subfamily, the Ichneumoninae, and this is obvious from keys to subfamilies in which separation of the two is sometimes difficult and revolves around two rather imperfect characters (Gauld 1984, 1995). There has only been one previous cladistic attempt to sort out the higher relationships of these and related taxa (Gokhman 1995) based on morphology the resulting trees were largely unresolved. Gokhman's study suggested that the Cryptinae might be paraphyletic with respect to the Ichneumoninae. To date molecular studies (Belshaw *et al.* 1998; Quicke *et al.* 2000) have suggested that these are probably closely related groups, being grouped with Eucerotinae, Adelognathinae and possibly Brachycyrtinae in an informal grouping of subfamilies, the Ichneumoniformes (Wahl 1993; Quicke *et al.* 2000). However, as too few taxa have been sequenced, these studies have failed to come to any firm conclusions as to the monophyly or otherwise of these two subfamilies.

We present here the first preliminary molecular phylogeny of the group that includes a wide range of cryptine genera. At present, relationships within the Cryptinae are obscured by a high level of homoplasy in the available morphological characters. With the inclusion of more taxa we hope to assess the validity of the tribes and many of the subtribes proposed by Townes (1970). Further, resolution of relationships within the Cryptinae will help to determine the groundplan biology of the subfamily and to test evolutionary scenarios for host shifts postulated by Gauld (1988).

Materials and Methods

Material analysed – The nuclear gene 28S was used for reconstructing the phylogeny of the cryptines and their relatives. The variable D2-3 region (750 bp) was sequenced for 52 ingroup taxa (Cryptinae and Ichneumoninae, including Alomyinae) and two outgroups, *Apechthis* (Pimplinae), chosen because it represents the Pimpliformes (Pimplinae), which is the putative sister group of the Ichneumoniformes (Quicke *et al.* 2000), and *Brachycyrtus* (Brachycyrtinae) because this subfamily is putatively a basal member of the Ichneumoniformes (Belshaw *et al.* 1998, Quicke *et al.* 2000).

Taxa included in analysis and their GenBank/EMBL accessions numbers (all are newly sequenced except those marked *) Pimplinae: *Apechthis* sp., UK, Z97934*. Brachycyrtinae: *Brachycyrtus convergens* Cushman, Brazil, AF423128. Ichneumoninae: *Alomya debellator* UK, Z83613*; *Crypteffigies albilarvatus* (Gravenhorst), UK, Z97919*; *Ichneumon* sp., UK, AF423125; *Listrodromus* sp., UK, AF423127; *Misetus oculatus* Wesmael AF418559, UK; *Virgichneumon maculicauda* (Perkins), UK, AF423126. Cryptinae: *Acroricnus stylator* Thunberg, UK, AF423148; *Agrothereutes abbreviator* (Fab.), UK, AF423150; *Aptesis nigrocincta* (Gravenhorst), UK, AF423172; *Aritranis* sp., UK, AF423152; *Arthula* sp., Papua New Guinea, AF423173; *Arhytis* sp., Malaysia, AF423145; *Ateleute* sp., Malaysia, AF423149; *Bathythrix* sp., Malaysia, AF423143; *Bathythrix pellucidator* (Gravenhorst), UK, AF423144; *Bentyra* sp., Malaysia, AF423165; *Cestrus* sp., Belize, AF423167; *Charitopes* sp., UK, AF423130; *Chirotica* sp. A, Malaysia, AF423157; *Chirotica* sp. B, Belize, AF423158; *Chrysocryptus* sp., Malaysia, AF423163; *Cisaris* sp., Malaysia, AF423139; *Coesula* sp., Malaysia, AF423131; *Cryptanura* sp., Brazil, AF423154; *Dagathia* sp., Malaysia, AF423129; *Demopheles corruptor* (Taschenberg), UK, AF423174; *Eurycryptus* sp., Malaysia, AF423146; *Endasys* sp., UK, AF423147; *Echthrus reluctator* (L.), UK, AF423164; *Gelis* sp., UK, AF423161; *Gnotus chionops* (Gravenhorst), UK, AF423153; *Goryphus* sp., Malaysia, AF423133; *Hadrocryptus* sp., Malaysia, AF423168; *Iaria* sp., Australia, AF423136; *Isdromas* sp., French Guyana, AF423156; *Lymeon* sp., Brazil, AF423162; *Mesoleptus* sp. A, El Salvador, AF423140; *Mesoleptus* sp. B, UK, AF423141; *Nematopodius debilis* (Ratzeburg), UK, AF423151; *Palpostilpnus* sp., Malaysia, AF423137; *Photocryptus* sp., Brazil, AF423155; *Phygadeuon* sp., UK, AF423142; *Platymystax* sp., Belize, AF423132; *Polytribax* sp., French Guyana, AF423170; *Priotomis* sp., Belize, AF423171; *Stenotes* sp., El Salvador, AF423159; *Stiromesostenus* sp., Australia, AF423135; *Stomacis* sp., Malaysia, AF423169; *Torbda* sp., Malaysia, AF423166; *Xanthocryptus* sp., Australia, AF423134; *Xenolytus* sp., El Salvador, AF423160; ?*Zurquilla* sp., Thailand AF423138 (this taxon closely resembles *Zurquilla* Gauld which was originally described from Costa Rica, though the latter genus was placed in the distantly related Tryphoninae).



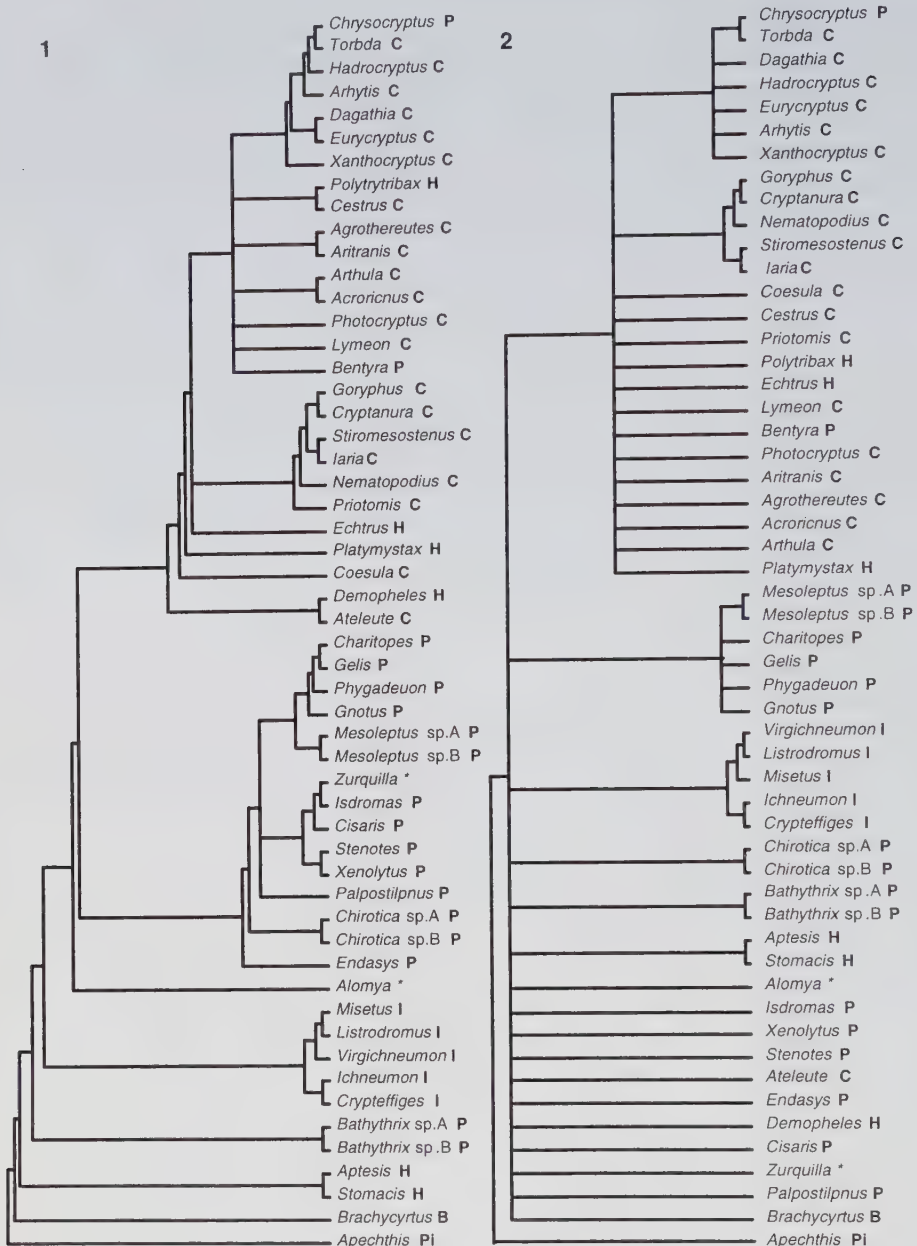
Sequence analysis. The data were analysed using Ward Wheeler's program, POY, that optimises characters straight onto the tree without alignment (Gladstein & Wheeler 1996-2000). The trees are rooted with *Apechthis* (Pimplinae). Analyses were carried out with the gap:substitution cost ratios of 2, 4, 6 and 8:1, using the following commands (annotated for explanation) norandomizeoutgroup (uses the first taxon in the data set as an outgroup; = *Apechthis* in this case); multibuild 6 (makes 6 builds in each round of tree-building); random 250 (executes 250 random addition sequence searches); fitchtrees (keeps randomly chosen trees in buffer in a way that maximises the differences within the saved subset of trees; Fitch, *in prep.*); treefuse (swapping subgroups of the same composition between trees; Goloboff 1999); fuselimit 25 (limits the number of tree-fusing pairs to 25); driftspr (performs one round of tree-drifting based on each spr search); numdriftspr 5 (sets the number of spr drift rounds); drifttbr (performs one round of tree-drifting based on an spr search); numdrifttbr 5 (sets the number of tbr drift rounds); noleading (allows for incomplete sequences with missing beginnings); trailinggap 1 (sets a weight of 1 to trailing gaps); slop 2 (checks all the cladograms found within 0.2% of the minimum tree length); checkslop 5 (in an extra round of tbr branch-swapping checks all trees within 0.5% length of current shortest tree); buildmaxtrees 2 (holds 2 trees in buffer while tree-building); maxtrees 2 (holds 2 trees in buffer at the end of a round of branch-swapping); holdmaxtrees 50 (in conjunction with maxtrees, holds 2 trees from the 50 shortest trees).

Results and Discussion

Although there was considerable variation in the detail of the trees obtained from the 4 different POY gap:substitution runs, there were a number of features that were robust to these search parameters (see Fig. 2). Firstly, the Ichneumoninae (excluding *Alomya*) always came out as monophyletic, and always within the Cryptinae, though sometimes with only *Bathythrix* more basal. No synonymy is being proposed here because we believe that considerably more data will be required to finally resolve the issue of the relationships of these two subfamilies.

Alomya (type genus of Alomyinae) has recently been transferred to the Ichneumoninae (Alomyini = Phaeogenini) (Wahl & Mason 1995), but it never comes next to *Misetus*, the other phaeogenine included in our data set. Thus our data support the notion that *Alomya* is a cryptine, but not that it is within the Ichneumoninae. It will be important to sequence other Alomyini, including *Colpognathus*, which Shaw & Bennett (2001) have recently shown to mummify its hosts in a similar fashion to *Alomya*.

Our trees are broadly congruent with the existing morphological tribal classification with the monophyly of the Cryptini and Phygadeuontini largely upheld. The Cryptini was found to be monophyletic with the inclusion of the hemigasterines (minus *Aptesis* and *Stomacis*) with a gap: substitution ratio of eight. Most Phygadeuontini came out as monophyletic and as a sister group to Cryptini when the gap:substitution ratio was high (Fig. 1) but in the strict consensus of trees from different gap:substitution ratio analyses it was broadly paraphyletic with respect to the Cryptini. The Hemigasterini were found to be an artificial assemblage, probably characterised by plesiomorphic characters. The most basal cryptine taxa in the analysis with the gap: substitution ratio of eight were the hemigasterine genera *Stomacis* + *Aptesis*. The other representatives of this tribe were mostly rather basal within the Cryptini (Fig. 1).



Figures 1–2 Strict consensus trees obtained from analyses of Cryptinae 28S rDNA D2+D3 regions using POY. 1, strict consensus of two trees obtained with gap:substitution cost ratio of 8 (chosen because sequences have few indels). 2, strict consensus of 14 trees obtained from POY runs with gap costs of 2, 4, 6 and 8. Abbreviations show current taxonomic placements: P=Phygadeuontini; H=Hemigasterini; C=Cryptini; I=Ichneumoninae; B=Brachycyrtinae; Pi=Pimplinae; * placed elsewhere earlier (see text)



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MOLECULAR ANALYSIS IN *EURYTOMA ROSAE* SPECIES-GROUP
(CHALCIDOIDEA: EURYTOMIDAE)

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Abstract – Taxonomic studies on parasitic Hymenoptera are based mainly on comparative morphology of adult wasps. However, separation of sibling species on the basis of imago morphology only sometimes is very difficult or even impossible. Claridge & Askew (1960) found such a species aggregate in *Eurytoma rosae* Nees which was grouped under single species name and they showed that it consists of six sibling species, between them, *Eurytoma rosae* Nees known to inhabit rose cynipid galls of the genus *Diplolepis*, and *E. brunniventris* Ratz. known to parasitize in oak cynipid galls only (Cynipidae: Cynipini). We have reared both species from rose and oak cynipid galls and the adult wasps were examined by using RAPD-testing. On the basis of DNA patterns it appeared that *E. rosae* includes two discrete groups, while *E. brunniventris* has been divided into three distinct groups. This separation closely depends on gall host specificity which from the eurytomid wasps were reared. It is possible that other sibling species can be find in *E. rosae* and *E. brunniventris*.

Key words: Eurytomidae, *Eurytoma rosae* group, sibling species, RAPD

Introduction

The *Eurytoma rosae* species aggregate belongs to parasitic wasps of the Eurytomidae family. Morphological uniformity is very characteristic for this *E. rosae*-group (Claridge & Askew 1960; Szelényi 1976; Claridge & Dawah 1994; Pujade-Villar 1994; Espejo-Noguera & Pujade-Villar 2000 and many others), especially after Zerova (1995) mentioned 30 species in this aggregate from the Palaearctic region.

Mayr (1878) recorded *E. rosae* Nees as a parasitoid reared from 56 different cynipid galls on *Rosa*, *Quercus*, *Acer* and *Hieracium*. Claridge & Askew (1960) after studying some peculiarities of the biology of the *E. rosae* species-group: egg shells, flying period of adults, host relationships, feeding behaviour etc., separated 6 species (Table 1).

Table 1 Six sibling species of *Eurytoma rosae* species aggregate
(after Claridge & Askew 1960)

Species	Host	Host Plant
<i>E. rosae</i>	<i>Periclistus</i> spp. in <i>Diplolepis rosae</i>	<i>Rosa</i>
<i>E. brunniventris</i>	Cynipid gall wasps & inquilines	<i>Quercus</i>
<i>E. curculionum</i>	Curculionidae (Coleoptera)	–
<i>E. centaurea</i>	<i>Phanacis centaurea</i> (Cynipidae)	<i>Centaurea</i>
<i>E. aciculata</i>	<i>Nematine</i> spp. (Tenthredinidae)	<i>Salix</i>
<i>E. hypochoeridis</i>	<i>Aulacidea hypochoeridis</i> (Cynipidae)	<i>Hypochoeridis</i>



They were unable to find any morphological characters for appreciable separation of *E. brunniventris* Ratz. and *E. rosae* Nees. Although some biological difference between the two species were found: *E. rosae* lives in rose galls and feeds only on inquilines, *Periclistus brandtii* Ratzeburg and *P. caninae* Hartig, and *E. brunniventris* inhabits oak galls and feeds mainly on inquilines or seldomly on cynipid gall-inducers. Claridge & Askew (1960) carried out some mating experiments between *E. brunniventris* and *E. rosae* which, however, were unsuccessful. The mating barrier indicated the existence of two biological species, *E. rosae* and *E. brunniventris*.

Zerova (1995) described two other species from oak cynipid galls: *E. adleriae* and *E. querceticola*. She separates her two newly described species on the basis of wing veins proportions. *Eurytoma adleriae* reared from galls of *Andricus conglomeratus* from Ukraine, has marginal vein slightly longer than stigmal, and nearly equal to postmarginal, while *E. querceticola* reared from galls of *Andricus quadrilineatus* from Moldavia, has marginal vein longer than stigmal and postmarginal. The identification of these *Eurytoma* species is very problematic and difficult because the proportions of the marginal, postmarginal and stigmal veins often strongly vary.

Therefore we decided to examine these species by using DNA techniques, particularly RAPD analysis, which appeared to be useful method to study closely related species (e.g. Hillis, Moritz & Mable 1996; Karp, Isaac & Ingram 1998).

Materials and Methods

The *Eurytoma* specimens were collected from three localities in Hungary: Ajka, Szeged and Tinnye (Figs 3, 4). Collected galls were put for individual laboratory rearing of eurytomids. Eurytomid species involved into the analysis are showed in Table 2.

Ten *E. rosae* specimens were reared from *Diplolepis rosae* (L.) galls collected from three places. *Eurytoma brunniventris* specimens were reared from 5 oak gall species. Two-two specimens were examined from each gall wasp species (*Andricus coriarius* Htg., *A. lucidus* Htg., *A. glutinosus* Gir., *A. multiplicatus* Gir., *Aphelonyx cerricola* Gir.). Out of this two main interested species, one specimens of *E. curculionum* Mayr was involved into the DNA analysis, which belongs to "rosae" group as well. Two specimens of *E. robusta* Mayr were used as an outgroup, reared from *Eurybia cardui* L. (Trypetidae). The living specimens were put in absolute alcohol and storing at -20°C until RAPD analysis.

Genomic DNA preparation

Specimens were take out from alcohol, the last was remove from the insect body. Each specimen was placed into 1.5 ml microtube and ground in extraction buffer (10 mM TRIS-Cl pH 8.2, 1 mM EDTA, 25 mM NaCl, 200 $\mu\text{g}/\text{ml}$ Proteinase K). This solution was kept at 37°C for 30 minutes (active Proteinase K), after was transferred to 95°C for 2 minutes (inactivation of Proteinase K). Samples were diluted to 100 μl final volume with sterile water treated with an ultra-pure water system. It is important to note that the insect debris does not impede PCR reaction.

Table 2 *Eurytoma* species involved into the analysis

Species	Code	Locality	Host	Host plant
<i>E. rosae</i>	ROS1	Ajka	<i>Diplolepis rosae</i>	<i>Rosa</i> sp.
	ROS2			
	ROS3			
	ROS4			
	ROS5			
	ROS6	Szeged		
	ROS7			
	ROS8			
	ROS9	Tinnye		
	ROS10			
<i>E. brunniventris</i>	BRN11	Ajka	<i>Andricus lucidus</i>	<i>Quercus pubescens</i>
	BRN12			
	BRN13		<i>Aphelonyx cerricola</i>	<i>Q. cerris</i>
	BRN14			
	BRN15		<i>Andricus glutinosus</i>	<i>Q. petraea</i>
	BRN16			
	BRN17	Szeged	<i>Andricus coriarius</i>	<i>Q. pubescens</i>
	BRN18			
	BRN19		<i>Andricus multiplicatus</i>	<i>Q. cerris</i>
	BRN20			
<i>E. curculionum</i>	CURC	Szeged	<i>Gymnetron</i> sp. (Curculionidae)	<i>Plantago maritima</i>
<i>E. robusta</i>	RSTA1	Ajka	<i>Eurybia cardui</i> (Trypetidae)	<i>Centaurea palustre</i>
	RSTA2			

RAPD assay

RAPD reactions were carried out following the method developed by Welsh & McClelland (1990) and Williams *et al.* (1990). The 25 µl reactions contained 18 µl buffer (1 × Taq polymerase buffer, 200 µM dNTPs, 3.5 mM MgCl), 1 unit of Taq polymerase, 25 pmoles primer and 4 µl template. PCR reaction preparation was made under a steril hood to reduce the possible contamination. Amplifications were performed in a thermal cycler M. J. Research PCR according to the programme given in Table 3. Reactions does not need overlaid with mineral oil, because this machine heat over as well. Control reaction with destillated water was used.

Table 3 PCR program used for DNA amplification

	Cycles 1-2	Cycles 3-4	Cycles 5-6	Cycles 7-8	Cycles 9-10	Cycles 11-12	Cycles 13-43
Denaturation	94°C for 30"	94°C for 30"	94°C for 30"	94°C for 30"	94°C for 30"	94°C for 30"	94°C for 30"
Annealing	45°C for 1'	44°C for 1'	43°C for 1'	42°C for 1'	41°C for 1'	40°C for 1'	37°C for 1'
Extension	72°C for 1'	72°C for 1'	72°C for 1'	72°C for 1'	72°C for 1'	72°C for 1'	72°C for 1'

The PCR products were electrophoresed in 2% TEA agarose gels at 100 mV, with DNA size marker (MMM), stained with ethidium bromide and photographed under UV light (312 nm). For RAPD analysis of all 23 specimens we used 9 primers (Operon Technologies):

Code	5' to 3'
OPC-07	GTCCCGACGA
OPC-13	AAGCCTCGTC
OPE-08	TCACCACGGT
OPP-19	GGGAAGGACA
OPT-20	GACCAATGCC
OPW-08	GA CTGCCTCT
OPAA-01	AGACGGCTCC
OPAA-02	GAGACCAGAC
OPAA-03	TTAGCGCCCC

The RAPD band profiles of *Eurytoma* specimens were analysed by free eyes because the pattern differences in groups were really sharp. The interpretations of pale bands are often ambiguous, therefore it is sometimes better to examine the gel photos by free eye by some experts.

Results

The RAPD reactions gave 5-20 bold bands in each column (Fig. 1). All 9 used primers gave similar results. The specimens were grouped on the basis of band patterns. PCR amplifications showed high reproducibility. Two specimens of *E. robusta*, used as an outgroup, were clearly separated from another specimens. It is important to say that the identification of *E. curculionum* adults without knowledge of their hosts is complicated. Although only one specimen was analysed, its band patterns were really rather different from others with all 9 primers.

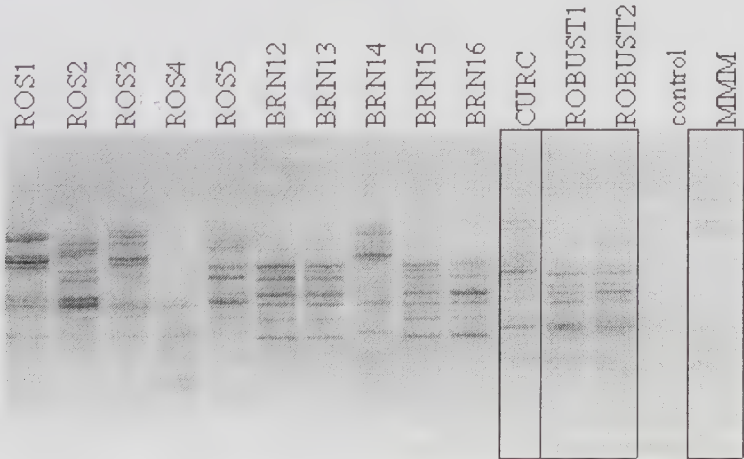


Figure 1 RAPD gel photo with OPAA-01 primer

Clear differences were found between *E. rosae* and *E. brunniventris*. Ten wasps reared from five oak gall wasp species clearly belong to three groups (Table 3).

Table 3 *Eurytoma brunniventris* groups based on RAPD analysis

Specimens	Host	Host plant	Group
BRN12	<i>Andricus lucidus</i>	<i>Q. pubescens</i>	I.
BRN13			
BRN15	<i>Andricus glutinosus</i>	<i>Q. petraea</i>	
BRN16			
BRN17	<i>Andricus coriarius</i>	<i>Q. pubescens</i>	
BRN18			II.
BRN19	<i>Andricus multiplicatus</i>	<i>Q. cerris</i>	
BRN20			III.
BRN14	<i>Aphelonyx cerricola</i>	<i>Q. cerris</i>	
BRN21			

It is remarkable that wasps of II and III groups were reared from galls which trophically associate with Turkey oak (*Quercus cerris*) only (Ambrus 1994; Melika, Csóka & Pujade-Villar 2000), which belongs to other subgenus of *Quercus* than all other oaks in Central Europe. Two specimens of group II were reared from *Andricus multiplicatus*, and other two specimens of group III were reared from *Aphelonyx cerricola* galls. Wasps of group I were reared from three gall species: *Andricus glutinosus*, *A. lucidus*, and *A. coriarius*, which trophically associate with *Quercus robur*, *O. petraea* and *Q. pubescens*.

The ten analysed *Eurytoma rosae* specimens were divided into two distinct groups. Collecting sites of two groups (A and B) are mixed (Table 4).

Table 4 *Eurytoma rosae* groups based on RAPD analysis

Specimens	Collecting Sites	Groups
ROS2	Ajka	A
ROS5	Ajka	
ROS7	Szeged	
ROS9	Tinnye	
ROS10	Tinnye	
ROS1	Ajka	B
ROS3	Ajka	
ROS4	Ajka	
ROS6	Szeged	
ROS8	Szeged	

Discussion

Despite of using few specimens, we have found significant polymorphism. Our results suggest interspecific difference because of considerable band differences which are striking (Fig. 2).



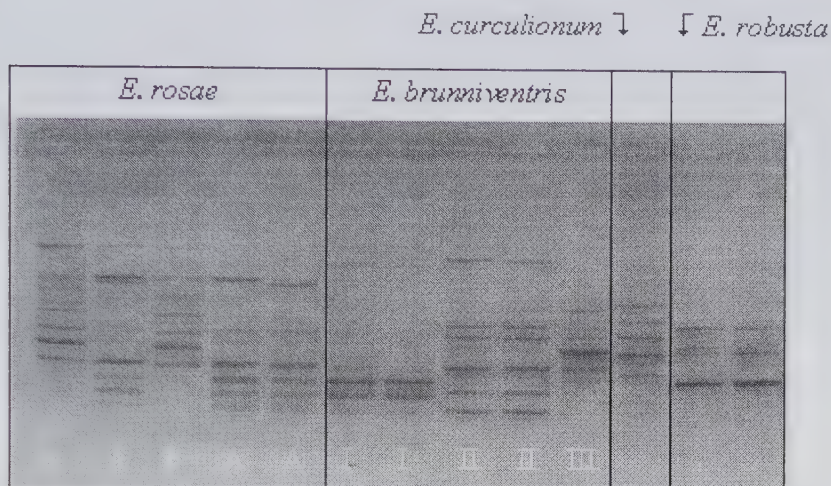


Figure 2 RAPD gel photo with OPW-08 primer



Figure 3 Map for *E. rosae* specimens



Figure 4 Map for *E. brunniventris* specimens

Beside the ten *E. rosae* specimens some others were analysed also with some primers. As a result the B genotype appeared from Tinnye as well. So, in all three localities there are both, A and B patterns. Collecting places are some hundred kilometers from one another. It is probably this two group (A and B) represent two species.

In the same way, the collecting sites and RAPD patterns of *E. brunniventris* specimens are shown in Figure 4. Specimens of group I were found in both collecting sites. Group II is derived only from Szeged, and group III only from Ajka. It is important to note there are no natural barriers for wasps' spreading. The area of their hosts are unbroken. If wasps of different groups mated, we could not find so heavy detachment in RAPD profiles at the same collecting sites. Consequently the three groups are likely to represent three species.

This work is only short insight into this species-group. Probably there are much more sibling species in this group. About 50 oak cynipid gall species have been listed which from eurytomids were reared in Central Europe. We examined only five gall hosts.

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PART 4

Kariosystematics



CHROMOSOMAL ANALYSIS OF THE SUPERFAMILIES ICHNEUMONOIDEA AND CHALCIDOIDEA (HYMENOPTERA)

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Abstract – A review of phylogenetic and taxonomic implications of karyological analysis of the Ichneumonoidea and Chalcidoidea is given. Higher chromosome numbers ($n = 14-21$) are characteristic for certain basal lineages in the Ichneumonidae and Braconidae, most of other members of the superfamily Ichneumonoidea having n values about 10-11. On the contrary, low chromosome numbers occur in the subfamily Aphidiinae and a few other groups of the Braconidae ($n = 3-9$). Comparatively high n values (8-12) are also found in all Mymaridae, Eurytomidae, Encyrtidae and some Aphelinidae, as opposed to many other Chalcidoidea with $n = 2-7$. The data presented suggest an overall reduction in chromosome numbers occurred in most of the Ichneumonoidea and Chalcidoidea. Moreover, further decreases in n values found in a few pairs of related genera of the Ichneumonidae represent their respective synapomorphies. Karyological studies can reveal groups of sibling species, as in *Anisopteromalus calandrae* (Howard) (Pteromalidae) with $n = 5$ and 7. Morphometric analysis has detected chromosomal differences in three pteromalid species of the genus *Nasonia*. Karyological characters can often mark isolated strains within the same morphospecies, as in *Ichneumon extensorius* L., *I. suspiciosus* Wesmael (both have forms with $2n = 24$ and 26), *Nasonia vitripennis* (Walker) ($n = 5$ and 6), *Aphidius ervi* Haliday and *Charmon cruentatus* Haliday (Braconidae) (both also have forms with $n = 5$ and 6).

Key words: chromosomes, karyotypes, Ichneumonoidea, Chalcidoidea, sibling species

Introduction

Although first karyotypic data for the Chalcidoidea and Ichneumonoidea were obtained at the beginning of the 20th century (Silvestri 1908; Hegner 1915), chromosomes of these superfamilies remained poorly known until last two or three decades (Goodpasture 1975; Goodpasture & Grissell 1975; Gokhman 1985 onwards). However, our knowledge of karyology of these groups has been substantially improved during recent years (see Gokhman & Quicke 1995; Gokhman 1997a; Quicke 1997; Gokhman 2000a). This paper summarizes chromosomal data for the Ichneumonoidea and Chalcidoidea obtained up to now as well as taxonomic implications of karyology and hypotheses on chromosomal evolution in these taxa.

At present, more than 170 species of the Ichneumonoidea are studied karyologically, including approximately 110 members of the family Ichneumonidae and 60 those of the Braconidae. Haploid chromosome number (n) values in this superfamily may vary from 3 to 21, having a clear mode at 11. The same modal number, $n = 11$, is also characteristic for the Ichneumonidae with $n = 6-21$. The lowest chromosome number in the family, $2n = 12$, has been observed in a tryphonine ichneumonid, *Netelia latungula* (Thomson) (Gokhman 2001), whereas $2n = 42$ was found in *Perithous scurra* (Panzer), a member of the subfamily Pimplinae (Gokhman & Kolesnichenko 1997). As for the majority of the family Braconidae, variation range of its n values is slightly smaller, i.e. from 3 to 20, with two modal ones of 7 and 10. $2n = 6$ has been found in *Aphidius* sp.

(Quicke 1997), whilst $n = 20$ was detected in an opiine braconid, *Diachasmimorpha longicaudata* (Ashmead) (Kitthawee *et al.* 1999). Despite many Ichneumonidae and Braconidae group around $n = 11$ and 10 respectively, members of some subfamilies have substantially higher chromosome numbers, i.e. 14-21 in the Ichneumonidae (Pimplinae, Microleptinae and Orthocentrinae) and 14-20 in the Braconidae (Doryctinae, Opiinae and Alysiinae) (Figs 1a, b). In the latter family, parasitic wasps of the subfamilies Aphidiinae, Charmontinae, Cheloninae and Exothecinae have lower chromosome numbers ($n = 3-9$) than those characteristic for many other Braconidae (Gokhman & Quicke 1995; Gokhman & Kolesnichenko 1998b; Quicke & Belshaw 1999; Silva-Junior *et al.* 2000).

Results and Discussion

Karyotypes of many Ichneumonoidea contain gradually decreasing in size bi-armed chromosomes, but a few species of this superfamily have considerable numbers of acrocentric chromosomes in their karyotypes. For example, *Venturia canescens* (Gravenhorst) is the only species of the Ichneumonidae having all its chromosomes acrocentric (Gokhman 2001). Moreover, in some other members of the family, e.g. in *Vulgichneumon saturatorius* (L.), chromosomes differ greatly in size (Gokhman 1987). Similar karyotypes have been recently found in a few Braconidae, such as *Chelonus inanitus* (L.) (Gokhman & Kolesnichenko 1998b).

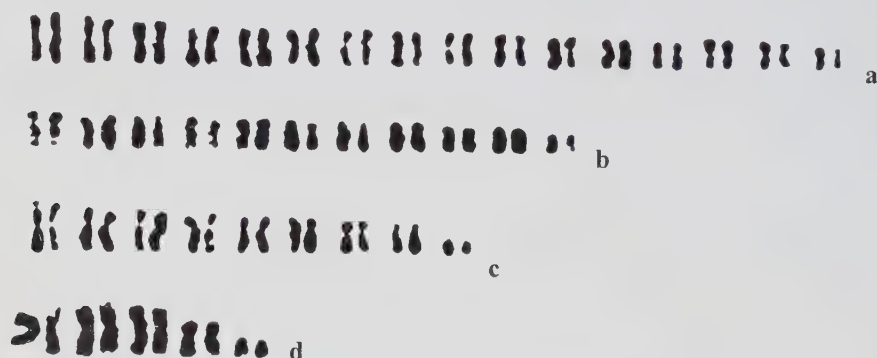


Figure 1 Mitotic karyograms of parasitic wasps: (a) *Dolichomitus messor* (Gravenhorst) (Ichneumonidae: Pimplinae), $2n = 32$; (b) *Colpognathus celerator* (Gravenhorst) (Ichneumonidae: Ichneumoninae), $2n = 22$; (c) *Anaphes listronoti* Huber (Mymaridae), $2n = 18$; (d) *Eupelmus urozonus* (Dalman) (Eupelmidae), $2n = 10$. Scale bar indicates 10 μm

Now chromosome numbers and other karyotypic features are also known for approximately 100 species of parasitic wasps belonging to the superfamily Chalcidoidea. Haploid chromosome numbers in this taxon have both lower values and variation range than those in the Ichneumonoidea, i.e. 2-12, with the modal number of 5. The lowest n value of 2 has been found in *Oligosita* sp. (Mymaridae) (Muramoto 1993), whereas the highest, $n = 12$, was detected in *Copidosoma buyssoni* (Mayr) (Encyrtidae) (Silvestri 1914). In the majority of chalcid wasps

haploid numbers may vary from 2 to 7 (mostly around 5-6), but all members of Mymaridae, Eurytomidae, Encyrtidae as well as some Aphelinidae have $n = 8-12$ (Gokhman 2000b) (Figs 1c, d).

As in the Ichneumonoidea, most members of the superfamily Chalcidoidea have bi-armed chromosomes of similar size. However, diploid karyotypes of many Eulophidae and some other chalcid wasps (e.g. a few Eupelmidae) contain large meta- or submetacentrics as well as a pair of small acrocentric chromosomes (Gokhman 2002) (Fig. 1d).

Since parasitic wasps with higher chromosome numbers generally belong to less advanced taxa of the Ichneumonoidea and Chalcidoidea, these values (i.e. $n = 14-17$ and $9-10$ respectively) are considered plesiomorphic. The data presented therefore suggest an overall reduction in chromosome numbers occurred in most of the Ichneumonoidea and Chalcidoidea. Even in the high-numbered taxa there are several species with low haploid numbers, e.g. *Alysia manducator* (Panzer) (Braconidae) with $n = 11$, the other Alysiinae having $n = 16-17$ (Gokhman & Kolesnichenko 1998a). Moreover, similar situations can be observed in some genera and species groups, and in these cases low n values are considered as synapomorphies. Specifically, *Oxyrrhexis* Foerster and *Polysphincta* Gravenhorst, both belonging to the tribe Polysphinctini (Ichneumonidae: Pimplinae), have n values of 8 and 9 respectively (Gokhman 2001), whereas in all other members of this subfamily $n = 14-21$. Similarly, ichneumonid genera *Patrocloides* Heinrich ($n = 8$) and *Pseudoamblyteles* Heinrich ($n = 9$) are synapomorphic for their lower chromosome numbers, as opposed to other members of the subtribe Ichneumonina with $n = 10-17$ (Gokhman 1997a). Analogously, autapomorphies can also be found in separate species within certain genera. For example, *Dirophanes callopus* (Wesmael) has $2n = 18$, whereas two other studied members of this genus, *D. fulvitaris* (Wesmael) and *D. invisor* (Thunberg), both have $2n = 20$. On the other hand, C-banded karyotypes of *D. callopus* and *D. invisor* mostly demonstrate pericentromeric heterochromatin, whilst in *D. fulvitaris* shorter arms of several chromosomes are also heterochromatic (Gokhman 1997b).

Chromosomal studies also revealed about ten groups of sibling species of parasitic wasps belonging to the Ichneumonoidea and Chalcidoidea, namely to the Ichneumonidae, Braconidae, Encyrtidae, Torymidae and Pteromalidae. Here I use the term "sibling species" in a broad sense, i.e. populations having no or little difference in their external morphology but obviously different by their karyotypic characteristics. These populations normally fall into following two classes:

(1) Populations with small but obvious and persisting differences in external morphology. These populations can usually be described as separate species (= sibling species in a narrow sense). Differences in chromosome number and other karyotypic characters in these species are often strong. Among the examples, there are two species groups of the Ichneumonidae, i.e. *Tycherus australogeminus* Gokhman ($2n = 22$) and *T. ischiomelinus* (Gravenhorst) ($2n = 18$) as well as *Aethecerus ranini* Gokhman ($2n = 22$) and *Ae. dispar* Wesmael ($2n = 24$) (Gokhman 1991). Another case can be found in *Anisopteromalus calandrae* (Howard) complex (Pteromalidae), where two distinct species with $n = 5$ and 7 were primarily detected on the basis of their karyotypic differences (see Gokhman & Timokhov, this volume).

(2) Populations without visible morphological differences. In this case, karyologically different populations usually cannot be described as separate species. Several groups of populations of that kind were found in the Ichneumonidae, namely in *Ichneumon extensorius* L. and *I. suspiciosus* Wesmael (both have forms with $2n = 24$ and 26) (Gokhman 1993). Similar forms having $2n = 10$ and 12 were recently revealed in two braconids, *Aphidius ervi* Haliday and *Charmon cruentatus*

Haliday (Gokhman 2000c and *unpubl. observations*). As for the Chalcidoidea, two different karyotypes with $n = 5$ and 6 were found in the well-known pteromalid, *Nasonia vitripennis* (Walker) (Goodpasture 1974). A more complex case was detected in *Copidosoma floridanum* (Ashmead) (Encyrtidae), where forms with $2n = 20$ and 22 seem to be morphologically identical (Hunter & Bartlett 1975; Strand & Ode 1990). However, a chromosome set with $2n = 16$ described in *C. floridanum* by some earlier workers (Patterson & Porter 1917 etc.) may belong to another distinctive species, probably to *C. bakeri* (Howard) or *C. truncatellum* (Dalman) (Noyes, *pers. comm.*).

Although karyological differences between closely related populations are usually weaker in the latter group, morphometric analysis has detected these differences in three members of the *Nasonia* species complex all having $n = 5$, i.e. *N. vitripennis*, *N. longicornis* Darling and *N. giraulti* Darling (Gokhman & Westendorff 2000). On the other hand, intergeneric morphometric differences between various Pteromalidae also having the same chromosome number, $n = 5$ (e.g. *Anisopteromalus calandrae* and *Nasonia vitripennis*), are much stronger (Gokhman, *unpubl. observations*).

All the data presented demonstrate that morphological and chromosomal divergences in parasitic Hymenoptera generally correlate to each other, i.e. the stronger is the difference in external morphology between certain forms, the larger it is in karyotypic features, and vice versa. However, this correlation is by no means complete. Indeed, there are many groups of well-differentiated species of parasitic wasps with virtually no karyotypic differences between them. On the other hand, the existence of superficially identical populations with strong chromosomal differences may indicate comparatively recent origins of those forms. Nevertheless, groups with the largest chromosomal variation between species always show persisting morphological differences.

Karyological methods can also reveal chromosomal polymorphisms in parasitic wasps, which involve both chromosome number and form. Among these, cases of variation in diploid numbers caused by non-disjunction of chromosomes (Gokhman 1989) as well as of that involving heterochromatic segments (Gokhman 1997b) are known. However, studies of a special class of B chromosomes known as "parasitic" ones are perhaps the most interesting.

There was discovered a particular sex ratio distorter in *Nasonia vitripennis* which caused complete male offspring and was found to be transmitted paternally. This PSR factor was first considered extrachromosomal (Werren *et al.* 1987), but subsequent studies demonstrated the presence of a smaller B chromosome responsible for the PSR effect (Nur *et al.* 1988; Werren 1991). Recently an analogous B chromosome was also found in *Trichogramma kaykai* Pinto et Stouthamer (Trichogrammatidae) (Stouthamer *et al.* 2001).

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CHROMOSOMES OF CHRYSIDOIDEA (HYMENOPTERA)

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Abstract – Despite chromosomes of only twelve species belonging to the Chrysidoidea have been studied to date, this superfamily represents a very divergent group in respect of its chromosome numbers ($n = 4-21$) and other karyotypic features. Moreover, n values found in all examined families, namely in Bethyridae ($n = 10$ and 14), Chrysididae ($n = 19$ and 21) and Dryinidae ($n = 4, 5$ and 7), do not overlap. Since higher chromosome numbers are suggested to be initial for the Chrysidoidea, lower n values detected in the Dryinidae, and probably also in the Bethyridae, are considered as their respective synapomorphies. Degrees of karyotypic difference between studied genera and species are generally consistent with levels of their taxonomic diversity.

Key words: chromosomes, karyotypes, Chrysidoidea

Introduction

Chromosomes of only twelve species belonging to the Chrysidoidea have been studied to date. Nevertheless, this superfamily represents a very divergent group in respect of its chromosome numbers and other karyotypic features, with its n values varying from 4 to 21 (Gokhman 2000, 2001). Moreover, variation ranges of chromosome numbers found in all examined chrysidoid families, namely in Bethyridae ($n = 10$ and 14), Chrysididae ($n = 19$ and 21) and Dryinidae ($n = 4, 5$ and 7), do not overlap (Table). Although no definite modal number is known for the Bethyridae, $n = 4$ and 19 constitute modes for the Dryinidae and Chrysididae respectively. In many species of the Chrysidoidea chromosomes gradually decrease in size, most of them being bi-armed. Although acrocentric chromosomes present in karyotypes of at least some Chrysididae, chromosome sets in the superfamily are generally symmetric. However, in *Anteon jurinearum* (= *A. brevicorne*) (Dryinidae) each chromosome pair differs greatly from all others either in its length or centromere position (Gokhman & Kolesnichenko 1998). Recently some details of meiosis were also studied in another two members of the genus *Anteon*, *A. gaullei* and *A. pubicorne* both having $n = 4$. Meiotic karyotypes of these species contained open (rod-like and cross-like) as well as closed bivalents, with the number of chiasmata per bivalent varying from one to three (Gokhman 2001). *Gonatopus clavipes* from the subfamily Gonatopodinae also has $n = 4$ and $2n = 8$, all its bivalents being circular (Fig. 1).

Results and Discussion

If chromosome numbers known for the Chrysidoidea are superimposed on the phylogenetic tree of the superfamily developed by Brothers & Carpenter (1993), the situation with an initial n value for all chrysidoids does not become more clear (Fig. 2). Indeed, a chromosome number of 10 to 19 is probably initial for the Bethyridae + Chrysididae, with an analogous n value for the whole subfamily laying between 4 and 19. However, since many other aculeate Hymenoptera, such as

Scolioidea, Pompiloidea, Vespoidea as well as most of Formicoidea, Sphecoidea and Apoidea, have modal haploid numbers around 15-17 and 25-26 (data compiled from many sources by the author), the initial n value for the Chrysidoidea may well lie within these limits. If this is true, lower chromosome numbers detected in the Dryinidae, and probably also in the Bethyidae, must be considered as their respective synapomorphies.

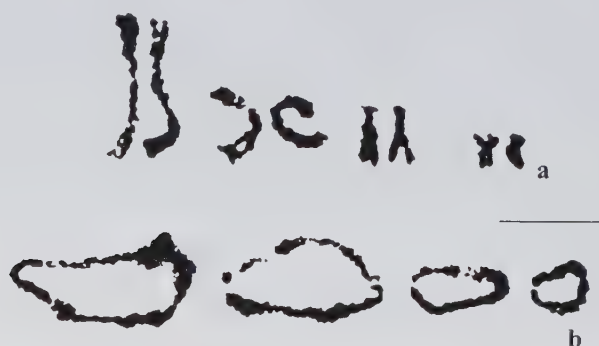


Figure 1 Karyograms of *Gonatopus clavipes*: (a) mitosis, $2n = 8$; (b) diplotene of meiosis, $n = 4$. Scale bars indicate $10 \mu\text{m}$

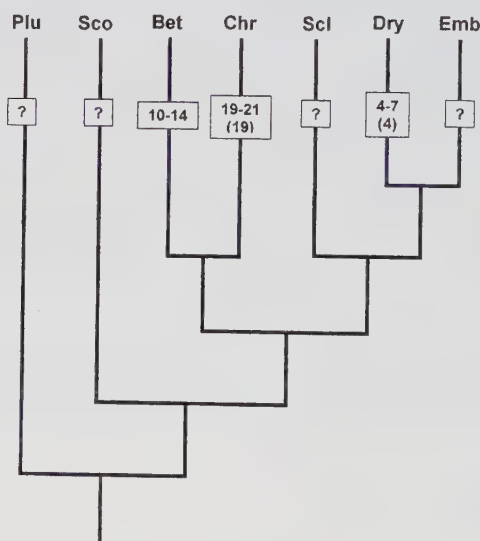


Figure 2 Phylogeny of the superfamily Chrysidoidea (after Brothers & Carpenter 1993) with variation ranges of haploid chromosome numbers superimposed on the scheme and modal n values shown in brackets. Abbreviations used: Plu – Plumariidae, Sco – Scolebythidae, Bet – Bethyidae, Chr – Chrysidae, Scl – Sclerogibbidae, Dry – Dryinidae, Emb – Embolemidae

Table Chromosome numbers in the Chrysidoidea. Unknown haploid/diploid values are extrapolated from the known ones and are given in brackets)

Species	Chromosome no.		Reference
	n	2n	
Family Bethylidae			
<i>Epyris niger</i> Westwood	(14)	28	Gokhman & Quicke 1995
<i>Laelius utilis</i> Cockerell	(10)	20	Gokhman & Quicke 1995
Family Chrysididae			
<i>Chrysis viridula</i> L.	(21)	42	Quicke & Gokhman 1996
<i>Hedychridium ardens</i> (Coquebert)	?(19)	?38	Quicke & Gokhman 1996
<i>H. roseum</i> (Rossi)	(19)	38	Quicke & Gokhman 1996
<i>Omalus djozanus hondonis</i> (Tsuneki)	(19)	38	Hoshiba & Imai 1993
Family Dryinidae			
<i>Anteon ephippiger</i> (Dalman)	(4)	8	Gokhman 2001
<i>A. jurinearum</i> Latreille	(5)	10	Gokhman & Kolesnichenko 1998
<i>A. gaullei</i> Kieffer	4	8	Gokhman 2001
<i>A. pubicorne</i> (Dalman)	4	8	Gokhman 2001
<i>Gonatopus clavipes</i> (Thunberg)	4	8	present paper
<i>Lonchodryinus ruficornis</i> (Dalman)	(7)	14	Gokhman 2001

Within each studied family of the Chrysidoidea, degrees of karyotypic difference between studied genera and species are generally consistent with levels of their taxonomic diversity. Indeed, two genera of the family Bethylidae have different chromosome numbers, $2n = 10$ and 14 (Gokhman & Quicke 1995). In the Chrysididae, *Hedychridium* and *Omalus* with $2n = 38$ both belong to the subfamily Hedychrinae, whereas *Chrysis* with $2n = 42$ belongs to the Chrysidinae (Quicke & Gokhman 1996). As for the Dryinidae, all but one studied species of this family belong to the Anteoninae. In this subfamily, members of the genus *Anteon* have $n = 4-5$, whilst $n = 7$ in a species of *Lonchodryinus*. Moreover, *A. ephippiger*, *A. gaullei* and *A. pubicorne* were referred to the genus *Chelogynus*, which was later merged to *Anteon* s. str. Different chromosome numbers found in *Anteon* s. l. may therefore reflect taxonomic heterogeneity of this genus. However, *Gonatopus clavipes* which is only distantly related to Anteoninae, also has $n = 4$ (Fig. 1), thus confirming this number to be initial for the whole family Dryinidae.

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TAXONOMIC STATUS OF POPULATIONS OF *ANISOPTEROMALUS CALANDRAE* (HOWARD) (HYMENOPTERA: PTEROMALIDAE) FROM RUSSIA, WESTERN EUROPE AND USA

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Abstract – A close study of *Anisopteromalus calandrae* (Howard) shows the existence of reproductive isolation between populations having different chromosome numbers. Strains with $n = 7$ are found on Curculionidae and Bruchidae, whilst populations having $n = 5$ normally parasitize Anobiidae. However, wasps of both groups can develop on alternative hosts. Females with $2n = 10$ have larger body size, preferring to oviposit on host prepupae and pupae, whereas those with $2n = 14$ are smaller, attacking last-instar larvae to pupae without any distinct preference. Differences in egg size between groups are correlated with those in female body length. The two forms also differ in their courtship patterns, including amplitude modulation of male sound signals in individuals with $n = 5$. Wasps with $2n = 10$ have lower egg production and female-biased sex ratio of the progeny, whilst those with $2n = 14$ have much higher fecundity and sex ratio close to 1:1. Preimaginal development is quicker in wasps with $n = 7$, though their eggs are destroyed by conspecific females in the case of superparasitism. Oviposition in females having $2n = 10$ is preceded by incomplete host paralysis and followed by marking of infested grains, whereas other wasps paralyze hosts more completely and never display kernel-marking behaviour. The differences observed are best interpreted in terms of r/K continuum. All the data presented demonstrate the existence of two separate species in the *A. calandrae* complex.

Key words: taxonomy, Hymenoptera, Pteromalidae, *Anisopteromalus calandrae*

Introduction

Anisopteromalus calandrae (Howard) (Hymenoptera: Pteromalidae) is a well-known cosmopolitan parasite of various stored-product pests (Hunter 1994; Quicke 1997). However, we have recently found that this taxon actually harbours populations with different chromosome numbers, which are also reproductively isolated and obviously differ in their sexual behaviour (Gokhman *et al.* 1998). The differences observed were later found to be correlated with many those in life-history characteristics and biological traits of these populations (Gokhman *et al.* 1999). In this paper we discuss the taxonomic status of various populations of *A. calandrae* originated from different countries.

Materials and Methods

Data on the origin of the strains of *A. calandrae* used in this study are given in Table 1. Parasitic wasps were identified by Zdenek Bouček (International Institute of Entomology, London,

UK) and Klarissa Dzhanokmen (Institute of Zoology, National Academy of Sciences, Almaty, Kazakhstan). Voucher specimens are deposited in the Zoological Museum, Moscow State University, Moscow, Russia. Morphology of adult wasps was analyzed using a binocular stereomicroscope. Chromosome preparations were made from cerebral ganglia of prepupae and ovaries of freshly eclosed adult females (see Gokhman *et al.* 1998 for description of the karyotyping procedure). Details of the techniques used for breeding and life-history studies are given in Gokhman *et al.* (1998, 1999). Statistical analysis was done using computer programs STATGRAPHICS version 5.0 and STATISTICA version 4.3.

Table 1 Origins of laboratory strains of *Anisopteromalus calandrae*

Strain	Origin		Original host	
	Region	Country	Family	Species
MSU	Moscow	Russia	Anobiidae	<i>Stegobium paniceum</i> (L.)
Moscow-2	Moscow	Russia	Anobiidae	<i>S. paniceum</i>
Michurinsk	Central Russia	Russia	Anobiidae	<i>S. paniceum</i>
Fresno	California	USA	Anobiidae	<i>Lasioderma serricorne</i> (F.)
Krasnodar-1	North Caucasus	Russia	Curculionidae	<i>Sitophilus granarius</i> (L.)
Krasnodar-2	North Caucasus	Russia	Curculionidae	<i>S. granarius</i>
ICSP	Ascot, Berkshire	UK	Bruchidae	<i>Callosobruchus chinensis</i> (L.)
ETH	Zürich	Switzerland	Curculionidae	<i>S. granarius</i>
Savannah	Georgia	USA	Curculionidae	<i>Sitophilus oryzae</i> (L.)
Bamberg	South Carolina	USA	Curculionidae	<i>S. oryzae</i>

Results

External morphology. Although *Anisopteromalus calandrae* is usually considered as a morphologically variable species, we managed to find a few invariant characters delimiting two obvious population entities. Among these features are: shape of the head in front view (triangular in the first group vs. rounded in the second), shape of last antennal segments of females (almost parallel-sided vs. distinctly clavate), features of the light-coloured area at the base of male metasoma (large and transparent, its lateral edges light vs. small and more obscure, its lateral edges brown) (Gokhman *et al.* 1998).

Karyological study. We have found $n = 5$ and $2n = 10$ in the first population group as well as $n = 7$ and $2n = 14$ in the second one (Table 2).

Courtship and mating behaviour. A comparative study of the MSU and ICSP strains revealed some important differences in their courtship and copulation patterns (see Gokhman *et al.* 1998 for details). Moreover, foreign males were always rejected by females, thus demonstrating the existence of reproductive isolation between populations. These data were further corroborated by those resulted from an analysis of male sound signals emitted during courtship (Fedina, *in litt.*).

Specifically, male song in the MSU population differs from that of the ICSP one by having a distinct amplitude modulation in its final part (Fig. 1). An extensive investigation of various strains has revealed two reproductively isolated population groups in *A. calandrae*, although strains belonging to the same group were fully compatible to each other (Table 3).

Table 2 Results of chromosome study of various strains of *Anisopteromalus calandrae*

Strain	No. of specimens studied		Chromosome no.	
	Males	Females	Haploid	Diploid
MSU	3	7	5	10
Moscow-2		1		10
Michurinsk		5		10
Fresno		11		10
Krasnodar-1	1	2	7	14
Krasnodar-2	1	2	7	14
ICSP	10	6	7	14
ETH	1	3	7	14
Savannah	1	3	7	14
Bamberg		2		14

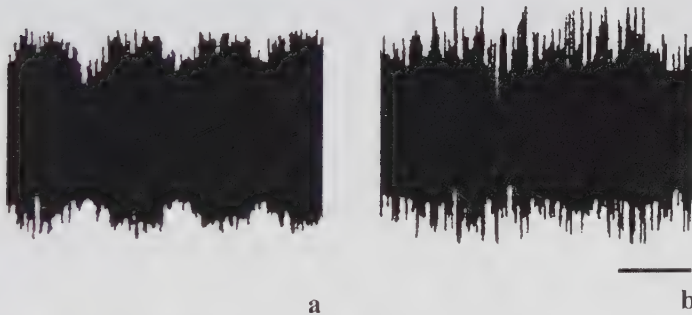


Figure 1 Fragments of the final part of male sound signals in the *A. calandrae* complex: a, MSU strain; b, ICSP strain. Scale bar indicates 0.2 sec

Hosts. As can be seen from Table 1, original hosts of *A. calandrae* used in the present study belong to Curculionidae and Anobiidae except for the ICSP strain, which was bred on a species of Bruchidae for many years. Moreover, we found that wasps belonging to both population groups were able to develop on alternative hosts (e. g. those using weevils could successfully parasitize anobiids, and vice versa). However, all studied strains showed a distinct preference of about 80 per cent for parasitizing initial hosts in host-choice experiments (i.e. *Sitophilus granarius* and *Lasioderma serricorne*) irrespective of time of their cultivation on preferred or alternative ones (Timokhov & Gokhman *in press*).

Life histories. Characteristics of life histories of the MSU and ICSP strains were studied in most detail on *S. granarius* (see Gokhman *et al.* 1999). Our experiments demonstrate that MSU females have larger body size and prefer to oviposit on host prepupae and pupae, whereas ICSP

ones are smaller and attack all host stages accessible under experimental conditions, from fourth-instar larvae to pupae, without any distinct preference. Differences in egg size between populations have obvious positive correlation with those in female body length of these wasps. Females of the ICSP strain begin to oviposit immediately after hatching, as opposed to the day following egression in the MSU population. MSU females have lower egg production and strongly female-biased sex ratio of the progeny, whilst wasps of the other strain have much higher fecundity and sex ratio close to 1:1. Preimaginal development is substantially quicker in the ICSP population, though its eggs are always destroyed by other females in the case of superparasitism. Oviposition in the MSU strain is usually preceded by incomplete host paralysis and followed by marking of infested grains, whereas ICSP wasps paralyse attacked hosts more completely and never display kernel-marking behaviour. Results of analogous experiments with the Fresno population are similar to those obtained with the MSU one except for the delayed oviposition, which is not observed in the former strain.

Table 3 Reproductive compatibility of males (horizontal rows) and females (vertical columns) of different strains of *A. calandreae* ("+" = normal copulation, "-" = lack of copulation, blank = no data available)

Strain	MSU	M2	M	F	K1	K2	ICSP	ETH	S	B
MSU	+		+	+	-	-	-	-	-	-
Moscow-2		+								
Michurinsk	+		+	+			-		-	
Fresno	+		+	+	-	-	-		-	-
Krasnodar-1	-			-	+	+	+		+	+
Krasnodar-2	-			-	+	+	+		+	+
ICSP	-			-	+	+	+	+	+	+
ETH							+	+		
Savannah	-		-	-	+	+	+		+	+
Bamberg	-		-	-	+	+	+		+	+

Discussion

Morphological, karyological, behavioural, acoustic and host data collectively suggest that *A. calandreae* harbours two distinct population groups. These entities are probably best distinguished by their karyotypic features, but have a lot of other differences (see above). Specifically, wasps with $n = 5$ (MSU, Moscow-2, Michurinsk and Fresno) constitute the first group, whereas those having $n = 7$ (Krasnodar-1, Krasnodar-2, ICSP, ETH, Savannah and Bamberg) form the second one. Given these two complexes are fully isolated from each other, we therefore conclude that they constitute two separate species. Moreover, we suppose that they have alternative life-history strategies. Since these species apparently differ in respect to their reproductive and competitive abilities, we also believe that these strategies are best interpreted in terms of r/K continuum (Gokhman *et al.* 1999). This assumption is further supported by an innate preference of the species with $n = 7$ to Curculionidae and of that having $n = 5$ to Anobiidae, because some ecological characteristics of these host groups can also be considered as respective elements of r and K strategies. Although sibling species with alternative life-history strategies which are interpretable

in terms of r/K continuum are probably described for the first time among parasitic wasps, a similar case of two thelytokous strains with different reproductive strategies has been recently detected in *Venturia canescens* (Gravenhorst) (Ichneumonidae) (Beck *et al.* 2000).

Since the type of *A. calandrae* is lost (Graham 1969; Bouček 1988), it is difficult to assign our material to any particular species. However, morphological features of the species having $n = 7$ fit the original description of *A. calandrae* better (Howard 1881), and therefore we are able to consider this species, at least provisionally, as the original *A. calandrae*.

The results obtained also have important practical implications because we managed to study a few strains widely used in biological experiments (e.g. Baker & Weaver 1993 onwards). As soon as identity of these populations is established, all their biological features can be assigned to the species having $n = 7$. The other one, however, seems to be examined less extensive, although some research has been undoubtedly done on this species (e.g. Johnson *et al.* 2000).

Plenty of information about these forms, e.g. that concerning their ecological relationships and geographical distribution, certainly awaits further studies. For example, they both inhabit North California (USA), although species with $n = 7$ occurs there in the wild, whereas that having $n = 5$ was found in this region only in warehouses and similar habitats (Heydon, *pers. comm.*).

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PART 5

Morphology



ANAGRUS AND OLIGOSITA: DIFFERENT STRATEGIES ADOPTED TO DEVELOP IN THE SAME HOST EGG (HYMENOPTERA: MYMARIDAE, TRICHOGRAMMATIDAE)

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Abstract – *Anagrus breviphragma* Soyka and *Oligosita krygeri* Girault, which develop in the same host egg (that of *Cicadella viridis* Linnaeus) were compared to assess the different strategies developed.

Key words: *Anagrus*, *Oligosita*, larvae, respiration, nutrition, host-ooparasitoid

Introduction

Host-ooparasitoid relationship expressed at two different levels: at parasitoid adulthood and at parasitoid young instars. Up till now, not only have host – preimaginal stage parasitoid relationships not been much investigated; parasitoid larval morphology, histology, ultrastructure and behaviour have also been disregarded, despite the fact that the success of female oviposition activity depends upon the capacity of the larvae to grow at the host's expense, and therefore their obvious importance for parasitoid use in biological control programs and for rearing them.

Here we try to analyse the most significant features that can influence the relationship between host and parasitoid immature stages:

- the degree of development of the egg embryo;
- the kind of structure of the chorion of the host egg.

Anagrus breviphragma Soyka (Fig. 1) and *Oligosita krygeri* Girault (Fig. 2), developing in *Cicadella viridis* Linnaeus eggs laid in the leaves of *Carex riparia* Curtis, can represent an example of different strategies.

Materials and Methods

Both *Anagrus breviphragma* Soyka (Hymenoptera: Mymaridae) and *Oligosita krygeri* Girault (Hymenoptera: Trichogrammatidae) were obtained from overwintering eggs of *C. viridis* in leaves of *Carex riparia* (Cyperaceae), in uncultivated areas along the Po river in Piacenza province Italy, during the winter months, from September to February.

Parasitized host eggs were kept at 20°C ($\pm 1^\circ\text{C}$) in Petri dishes on filter paper moistened with physiological solution. For morphological observations, specimens dehydrated in a graded ethanol series, dried to the critical point with CO₂ and metallized with gold, were studied under a Hitachi S 2300 scanning electronic microscope.

For histological and ultrastructure observations, specimens still in the host or extracted from it, were fixed in Karnowsky's (1965) solution, postfixed in 1% OsO₄ in cacodylate buffer, dehydrated

in a graded ethanol series until 90%, block stained with 1% uranylacetate in 95% alcohol, passed in absolute alcohol, and embedded through propylene oxide in Epon-Araldite. Sections, about 70 nm thick, sequentially stained with uranylacetate and lead citrate were examined through a Jeol JEM-1200EXII transmission electron microscope.

Results and Discussion

As far as the alimentary apparatus and feeding behaviour are concerned, both *A. breviphragma* and *O. krygeri* larvae have a mouth that is basically a hole with a plug: liquid food enters by means of a different pressure and it is necessary to actively stop it from entering instead of actively introducing it into the alimentary channel. Both parasitoids present a salivary duct opening, bordered by circular muscles and both show mandibles not located around the mouth opening: those of *Anagrus* are curved, long, acuminate and fixed (Fig. 3) while those of *Oligosita* are very short, blunt-tipped, exodont and retractable (Fig. 4).

The behaviour of the larvae is different. *Anagrus* first instar larvae do not move and probably breathe and nourish themselves by means of the cuticle while, second instar larvae continue to bend and straighten and curl (Moratorio & Chiappini 1995). Thanks to these movements and to the presence of the mandibles, they can break down the host embryo tissues, when already formed, and render them liquid so as to be able to use them to nourish themselves. On the opposite, all larval instars of *Oligosita* are almost completely immobile: they only show some activity for a few hours during which they swallow the egg content (Bakkendorf 1934), which they cannot alter.

Therefore, in *C. viridis* eggs parasitized by the *Anagrus* the death of the embryo, when already present, is caused by the 2nd instar larvae of *Anagrus*, as it has been observed in many cases that the embryo continues its development until the parasitoid becomes a second instar larva. On the contrary the larvae of *Oligosita* have been observed to swallow the egg content so quickly as to compromise its chance of developing into an embryo. Young *C. viridis* larvae are born if the female has oviposited in an egg that is too developed.

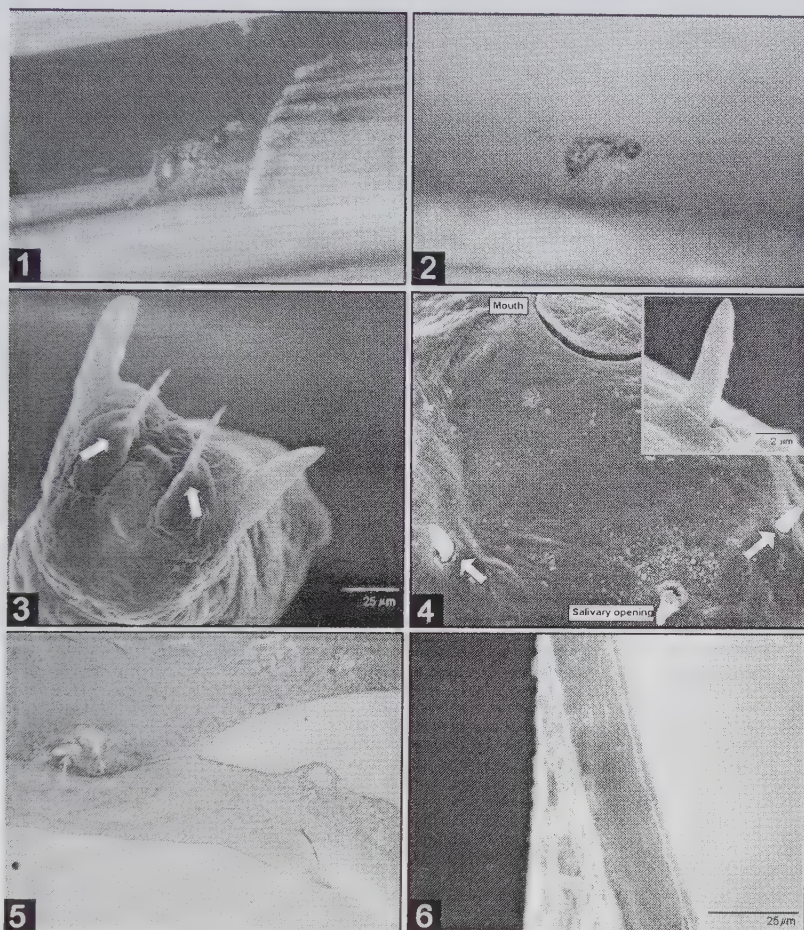
The consequence is that *Anagrus* females have far fewer constraints to obey: they can parasitize *C. viridis* eggs at almost any time as their larvae can use eggs with almost any degree of embryonic development. On the other hand *Oligosita* females can parasitize only eggs that contain just yolk; they must decide which are the best eggs to oviposit into, as the larvae do not show enough plasticity to cope with a "non optimal situation".

As far as respiration is concerned, neither *A. breviphragma* nor *O. krygeri* larvae have a respiratory apparatus, like all Mymaridae and Trichogrammatidae, but while *Anagrus* pupa has not tracheae *Oligosita* has (Fig. 5) and both of them pupate inside the host egg.

The egg of *C. viridis* has a chorion with no aeropiles to let free air in and so thin (about 2 μ m thick) that, if it desiccates, can collapse very easily, trapping and squeezing the parasitoids inside it (Fig. 6).

Also in this case the parasitoids behave differently. *A. breviphragma* larvae may or may not entirely devour the egg mass, but in any case, the pupae are still surrounded by a liquid which fills the egg and determine an internal pressure that keeps it turgid. *O. krygeri* larvae entirely devour the egg mass, and the pupae occupy all the space inside the egg without any liquid left around them so that there is no internal pressure and the thin chorion of the egg may collapse.

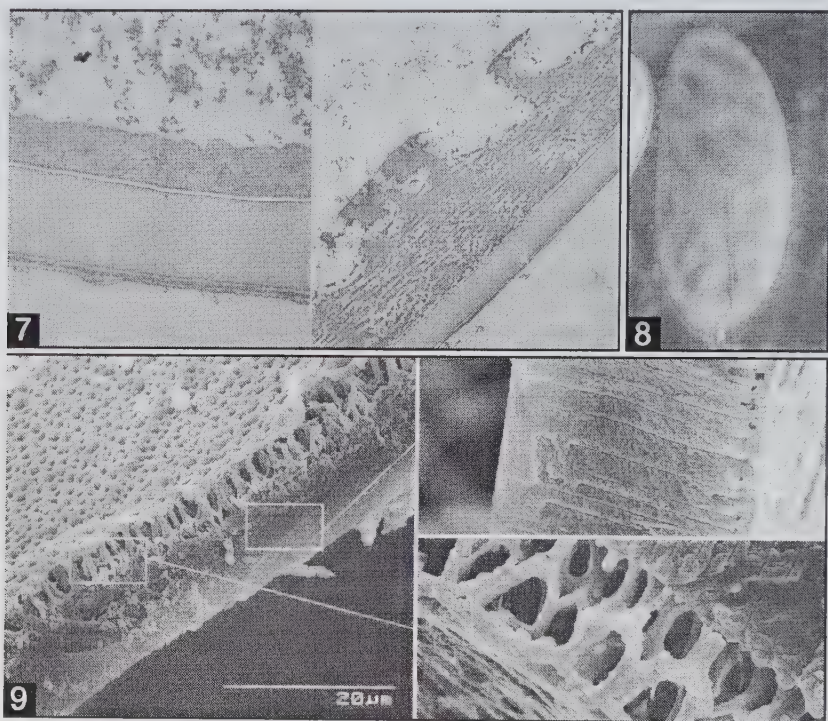
Therefore, *Oligosita* does build a cocoon to prevent the egg from collapsing, when dehydrating in order to let free air in for the pupa. *Anagrus*, on the other hand, does not build a cocoon as it does not need free air and the internal pressure would prevent the egg from collapsing (Fig. 7).



Figures 1–6 1, *Anagrus breviphragma* female ovipositing in *C. viridis* eggs in *Carex riparia* leaf; 2, *Oligosita krygeri* female ovipositing in *C. viridis* eggs in *Carex riparia* leaf; 3, Scanning electron micrograph of *Anagrus* second instar larva cephalic portion (arrows indicate the mandibles); 4, Scanning electron micrograph of *Oligosita* mature larva cephalic portion (the arrows indicate the mandibles, one of them enlarged in the box); 5, Transmission electron micrograph of *Oligosita* pupa cross-section (tracheae are indicated by arrows); 6, Scanning electron micrograph of the *C. viridis* egg cross-section, showing the thin and uniform chorion

Oligosita mandibles that seemed to have no function in the feeding process, could be used to pierce the *Cicadella* egg chorion in order to let free air in more easily, as it has been demonstrated by Laudonia & Viggiani (1986) and Colazza & Bin (1992) for *Edovum puttleri* 3rd larval instar, but so far we have not been able to find any evidence of this.

A further confirmation of the previous interpretation can be found if we compare *Oligosita krygeri* to *Oligosita phaneropterae* Viggiani, a very similar species, developing in eggs of a different species (*Phaneroptera nana nana* Fieb.) (Fig. 8): the larvae of both species develop as gregarious and do not have a tracheal system, in addition both species pupate inside the host egg and their pupae have tracheae. Nevertheless *O. krygeri* builds a cocoon but *O. phaneropterae* does not.



Figures 7–9 7, Transmission electron micrograph of *C. viridis* egg cross-section, parasitized by *Anagrus breviphragma* (top) and *Oligosita krygeri* (bottom) (the cocoon is recognisable inside the latter); 8, Scheme of the characteristic swellings on the external *Carex* leaf surface due to the presence of *C. viridis* and *P. nana nana* eggs (top) and the different aspect of the two kind of eggs as one can see them when one of the two epidermis has been lifted; 9, Scanning electron micrographs of the *P. nana nana* egg cross-section, showing the structure of the entire chorion (left) and the enlargements of the perforated layer (top) and Pilaster layer (bottom)

Phaneroptera nana nana egg has a very thick chorion, constituted of a layer about 13 μm thick, perforated by numerous canals regularly arranged at a distance of about 0,7 μm from each other. These canals end in a more external layer, about 4 μm thick, formed by pilasters united in such a way as to form a sort of mesh, and covered by a thin perforated membrane (Fig. 9). Therefore, a *P. nana nana* egg, when its internal material has been completely consumed (usually about 20 parasitoids develop in one egg), and the parasitoids inside it pupate, can be filled with air from the outside. In addition, *P. nana nana* egg has a chorion so thick that it does not collapse easily.

On the opposite, as we have seen, *C. viridis* egg chorion has no aeropiles so to let free air in and is so thin that it can collapse very easily.

Therefore if *O. phaneropterae* already has free air available when passing from the larval stage to that of pupa and does not need to build a cocoon, *O. krygeri* needs to assure itself free air when passing from the larval stage to that of pupa and does build a cocoon.

Conclusions

Internal egg parasitoids dispose of limited food resources and have to face another major problem: the respiration.

In this study, we have considered how the major aspects of respiration and nutrition are dealt with in the two parasitoids studied, in relation to the developmental degree of their host and we have analysed the different solution adopted.

We have not considered the aspect of desiccation but we know that the vitelline membrane or the serosal cuticle that can be produced during embryonic development, change the egg's permeability to water (Pak *et al.* 1990). Therefore, the developmental degree of the host parasitized is an important aspect to consider also in relation to dehydration.

We also haven't take into account the aspect of host-defence as it has been assessed that this is not a problem that oophagous parasitoid must face: the food of the species that are parasitoids in eggs "is unable to react and defend itself against the attacks of their enemies" (Salt 1968) and, therefore, both the young parasitoid stages do not have to worry about how to escape host defences and the ovipositing female does not have to bother about immobilising or conditioning the host (Mellini 1993).

In fact, in our study, we have verified that neither females act any host conditioning.

Nevertheless, Locci *et al.* (1998) demonstrated that "at least some of the cells released by the yolk sac may be embryonic hemocytes" which "are capable of adhering onto the substratum by protruding several pseudopodia along the cell periphery". It is therefore correct to wonder if these active haemocytes, present at the end of embryonic development, might also be involved in embryo defence.

Host defence and dehydration are therefore two other important aspects to consider in relation to the embryo development degree at which the parasitoids can attack the host eggs.

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OVIPOSITOR SENSORY STRUCTURES OF *ANAGRUS BREVIPHAGMA* SOYKA AND THEIR POSSIBLE SIGNIFICANCE (HYMENOPTERA: MYMARIDAE)

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Abstract – *Anagrus* ovipositor was first studied under a Scanning Electron Microscope to map all those structures that could represent sensilla and subsequently at Transmission Electron Microscope to verify their ultrastructure and therefore their significance as sensory structures. Five sensilla were found on first valvulae: -two proprioceptors; a "hooked peg", curved towards ovipositor base and inserted in a pit, on the external surface of the first valvulae, proximal to serration; a second peg which comes out laterally in the middle of the serration of the first valvulae; another peg on the internal surface at the point where the aulax of the first valvulae begins. No sensilla were found on second valvulae and only one mechanoreceptor seta on third ones.

Key Words: *Anagrus*, ovipositor, sensilla, ultrastructure, Mymaridae

Introduction

Many studies have given consideration to the reproductive methods of parasitoid Hymenoptera in relation to their search for and parasitization of the host. Host-parasite interactions take place at various levels: from the attraction of the parasitoid to sites where it is likely to find a host, and where it can therefore begin a careful search for the stages to parasitize, till the laying of the eggs. In all the early phases of the search, up to the contact with the stage for parasitization, the parasitoid uses principally the sensilla on its antennae, whereas once it has begun the actual phase of probing, it tests the host also with the ovipositor in order to evaluate its condition. This phase of acceptance of the host immediately precedes the act of laying the egg.

Anagrus breviphagma Soyka is an oophagous parasitoid that can parasitize various species of cicadas, with eggs that may vary greatly in their dimensions.

The egg-laying patterns of *A. breviphagma* Soyka were investigated by Moratorio (1990), who described them in detail. In smaller eggs, the parasitoids lay only one egg and refuse the host, after testing it with the ovipositor, if it has already been parasitized. In larger eggs, the parasitoids lay more than one egg and may refuse the host or not, after testing it with the ovipositor, if it has already been parasitized.

It is therefore of particular interest to study ovipositor sensory structures to better understand *Anagrus breviphagma* reproductive behaviour.

Materials and Methods

Adult females of *Anagrus breviphragma* Soyka, just emerged from the host eggs of *Cicadella viridis* L., were dehydrated through graded ethanol series, CO₂ critical-point dried, gold coated, and studied under a Hitachi S 2300 scanning electron microscope, in order to locate and inventory all sensory structures detectable that way, especially chemoreceptors.

For transmission electron microscopy, entire specimens were soaked in Karnowsky's (1965) fixative solution for three hours, next rinsed in cacodylate buffer several times and left in it overnight at 4°C, then postfixed in 1% OsO₄ in cacodylate buffer for one hour and fifteen minutes, rinsed again in cacodylate buffer, dehydrated in a graded ethanol series until 90%, block stained with 1% uranylacetate in 95% alcohol for forty minutes, two more passages in absolute alcohol, and embedded through propylene oxide in Epon-Araldite. Sections, about 70 nm thick, sequentially stained with uranylacetate and lead citrate were examined through a Jeol JEM-1200EXII transmission electron microscope.

Results and Discussion

The structure of the ovipositor in *Anagrus* is that typical of Hymenoptera Terebrantia with three pairs of valvulae (Snodgrass 1933), the first and second of which constitute the ovipositor proper and the third are the "ovipositor sheaths" (Quicke *et al.* 1999).

Externally and distally, the ovipositor sheaths, the two independent and distal lobes of the 9th gonocoxites which protect the ovipositor proper (Fig. 1), bear one long bristle each, which is a tactile sensillum (Fig. 1 – white arrow). Internally they appear to be lined with an enormous quantity of shorter and not innervated setae (Fig. 2). Here, the cuticle is thinner than externally and perforated by numerous pores (Fig. 3); inside gland cells are present.

The single piece constituting the second (upper) valvulae and the two separate pieces representing the first (lower) valvulae are connected by the "olistheter" mechanism (Quicke *et al.* 1999), while the ventral edges of the two first valvulae are rolled together in a curl that allows them to stretch apart when the egg passes through the egg channel (King & Copland 1969) (Fig. 4). Both the 1st and 2nd valvulae are serrated on their tips (Fig. 2).

The internal surface of the egg canal, formed by the inner wall of the lower valvulae alone, is furnished with finger-like processes, distally pushed aside to form a pouch (Fig. 6 – arrows), which push the egg along during oviposition (Quicke *et al.* 1999).

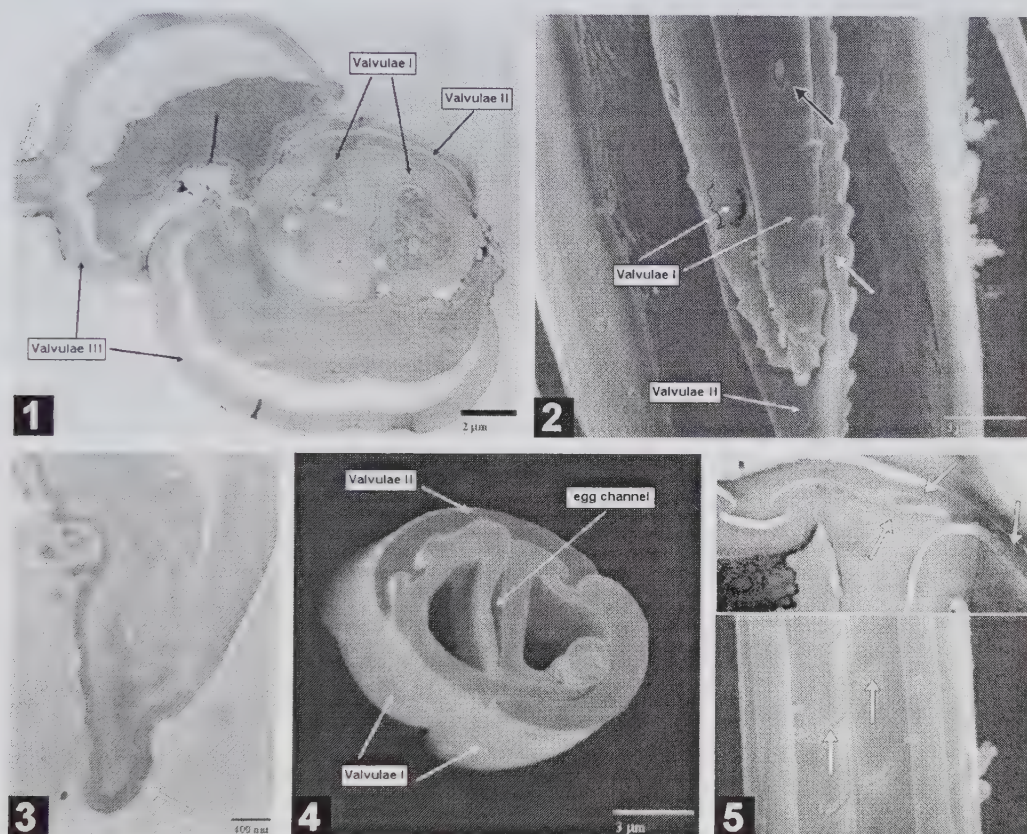
On the opposite internal surfaces of the 1st and 2nd valvulae, numerous lines of little round plates are present (Fig. 5 – arrows), these structures have only a mechanical function as no nervous termination has been detected.

Externally, no other cuticular structure can be detected on the 2nd valvulae, nor any nervous termination internally.

On the other hand, numerous sensilla are present on each of the 1st valvulae. From the ovipositor base to its distal apex, the first sensillum is situated roughly in the middle of their external surface and is not evident at SEM observation. It is a campaniform sensillum with a single dendritic segment which forms a ciliary constriction just before entering the valvula cuticle and which ends with a tubular body under an external apparatus of finer and more electron-dense cuticle (Fig. 7 – arrows). It probably has a proprioceptive function which measures the tension of

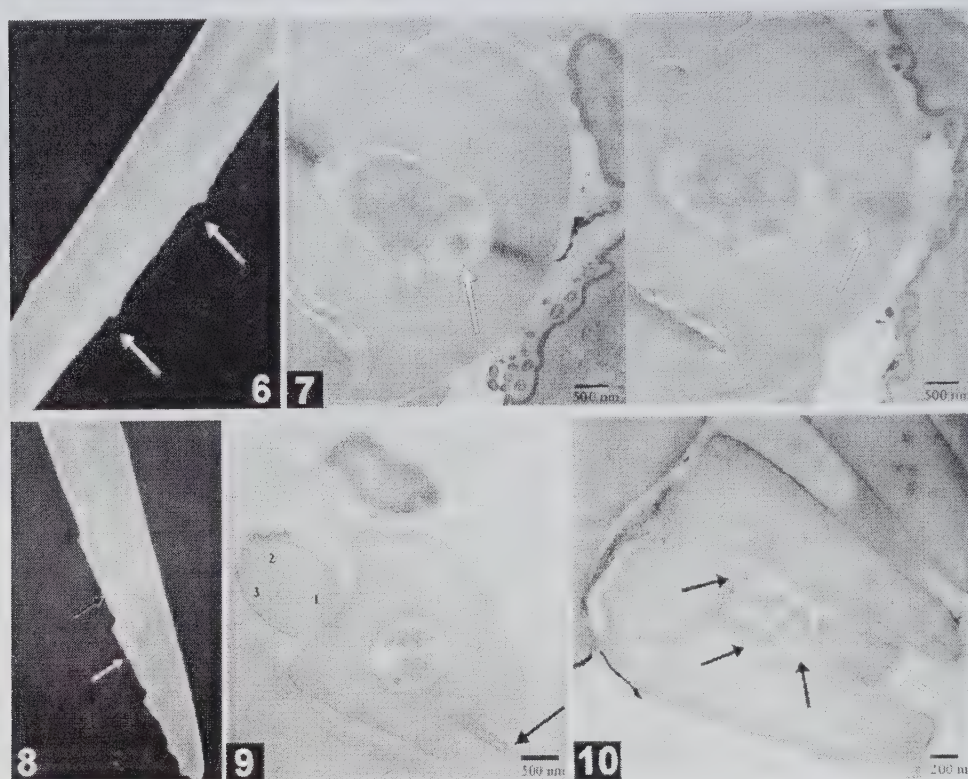
the ovipositor when it penetrates the host egg. A second campaniform sensillum is situated about 20 μm more distally, in the same position.

The third sensillum, situated almost in the same position as the previous ones but a little more distally, just before the beginning of the serration, is a hooked peg, almost completely sunk in a pit (Fig. 2 – black arrow). It is a mechanoreceptor with a single external dendritic segment terminating with a tubular body.



Figures 1–5 *Anagrus breviphagma* female. 1, Transmission electron micrograph of ovipositor cross section. The white arrow indicates the tactile sensillum on the third valvulae; 2, Scanning electron micrograph of the ovipositor distal portion. The black arrow indicates the third sensillum present on the first valvulae, a hooked peg sunk in a pit, while the white arrow indicates the fifth sensillum of the first valvulae, a stout and curved peg sticking out laterally in the middle of serration; 3, Transmission electron micrograph of third valvulae lateral edge cross-section; the arrow indicates one of the pore present through the thinner portion of the cuticle; 4, Scanning electron micrograph of the ovipositor cross-section, showing the relative position of the first and second valvulae; 5, Transmission electron micrograph of first and second valvulae cross-section at the level of the little round plates (white arrows) present on the opposite internal surfaces, and scanning electron micrograph of the second valvulae internal surface where lines of the same little round plates are visible (white arrows)

The cuticular apparatus of the fourth sensillum consists of a thin peg, set at the end of the aulax of the olistheter (Fig. 8 – black arrow). Six external dendritic segments reach beneath the valvula cuticle, but it seems that only one, corresponding to the tubular body, crosses it to enter the peg (Fig. 9 – black arrow).



Figures 6–10 *Anagrus breviphragma*. 6, Scanning electron micrograph of the 1st valvulae internal surfaces. The white arrows indicate the finger-like processes distally pushed aside to form a pouch, present on the internal surface lining the egg-channel; 7, Transmission electron micrograph of first valvulae cross-section at first campaniform sensillum level. The arrows indicate the tubular body still inside the first valvula lumen (left section, more proximal) and entering the cuticle (right section) under an external apparatus of finer and more electron-dense cuticle; 8, Scanning electron micrograph of the first valvulae distal portion. The black arrow indicates the fourth sensillum, a thin peg set at the end of the groove with which the ridge of the second valvulae interlocks, while the white arrow indicates the fifth sensillum, a stout and curved peg sticking out laterally in the middle of serration; 9, Transmission electron micrograph of the cross-section of the first valvulae, the one on the left at a more distal level. The black arrow indicates the fourth sensillum. The numbers indicate the pores where the latest three, of the five round electrodense structures, end; 10, Transmission electron micrograph of first valvulae cross-section. The black arrows indicate the latest three of the five round electrodense structures, while the white arrow indicates the fifth sensillum, a stout and curved peg sticking out laterally in the middle of serration; its external dendritic segment, corresponding to the tubular body, entering the cuticular apparatus of the peg, is detectable

The cuticular apparatus of the fifth sensillum is a stout and curved peg sticking out laterally in the middle of serration (Figs 2 and 8 – white arrows). Five external dendritic segments reach beneath the valvula cuticle, but it seems that the one, corresponding to the tubular body, perhaps together with another one, enters the peg (Fig. 10 – white arrow).

Both these sensilla, presenting a tubular body and respectively five and six other dendritic segments, display an organisation similar to chemosensory ones, but we could detect no pores to validate this hypothesis.

In addition, five round electrodense structures, always present along the whole length of the 1st valvulae, seem to enter the cuticle: one between the first two campaniformia, one in correspondence of the third sensillum and three at the distal apex of the valvula (Fig. 10 – black arrows), where three corresponding pores could be detected (Fig. 9 – numbers).

In all of these sensilla the sensory neurones perycarions were not found inside the valvulae: they probably lie in the abdomen sending the inner dendritic segments, discernible by the presence of microtubules and mitochondria, inside and along the first valvulae.

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THE MORPHOLOGY OF THE AEDEAGUS AS A TOOL USEFUL FOR CHARACTERISING THE SPECIES-GROUPS OF *IDRIS* FOERSTER (HYMENOPTERA: SCELIONIDAE)

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Abstract – In the genus *Idris*, including 169 described species egg-parasitoids of spiders, the *melleus*-group is the only defined species-group. The morphology of the copulatory organ, here analysed in 17 Palearctic species, could help to characterise the species-groups of this genus. The aedeagus of each of the examined species is distinguishable by: a) ratio of aedeagal lobe, digiti, aedeago-volsellar shaft and basal ring, b) number, shape and length of digital teeth. Among these species the authors recognise four different types of aedeagus ('flavicornis', 'rufescens', 'semicastaneus' and 'zonatus' types), differing in the shape and sclerotisation of the aedeagal lobe, and in the shape of the rest of the aedeago-volsellar shaft. The general shape of the copulatory organ should not be exclusive of just one species-group, as the presence of the 'rufescens' and 'flavicornis' types of aedeagus also in species considered belonging to other groups seems to confirm.

Key words: copulatory organ, subgeneric groups, egg-parasitoids of spiders

Introduction

The genus *Idris* includes 169 described species (Jonhson 1992; Masner & Denis 1996), and a conspicuous number of undescribed species distributed in all zoogeographical regions (Masner 1976). The species, whose hosts are known, are parasitoids of eggs of spiders (Eason *et al.* 1967; Bradoo 1972; Fitton *et al.* 1987). In spite of the large number of described species, the only defined species-group is the *melleus*-group (Masner & Denis 1996). This is probably due to the still unsatisfactory knowledge of the morphology of the *Idris* species. Huggert (1979) grouped the described West Palearctic species of this genus in some species-groups just naming them, but without providing a diagnosis. In the same paper this author drew and described the aedeagi of only two species (*Idris flavicornis* Foester and *I. rufescens* (Kieffer)), considering the first one essentially similar to the one of *I. psammon* Szabó, moreover noting the peculiarity of the second one. In one genus of Scelionidae (i.e. *Telenomus* Haliday) the morphology of the aedeagus is greatly variable (Nixon 1935; Polaszek & Kimani 1990), whereas in the entire tribe Gryonini the morphology of the copulatory organ is very homogeneous.

The aim of this study was to investigate whether the morphology of the aedeagus could be a character useful to define subgeneric groups also in the genus *Idris*.



Materials and Methods

The aedeagi, when extruded, were detached directly from the gaster of card mounted specimens; otherwise the gaster was dissected after macerating it in KOH; then the copulatory organs were mounted on slide using Faure gum. They were detached from 26 specimens belonging to 17 Palearctic species, as following: one specimen each of *I. piceiventris* (Kieffer), *I. nigroclavatus* (Kieffer), *I. priesneri* Huggert (these first three species identified by L. Huggert in 1976), *I. glabratus* Huggert, *I. flavicornis*, *I. psammon*, *I. semiflavus* (Kieffer), *I. aureonitens* Szabó, *I. zonatus* (Kieffer), and *I. meridionalis* Masner; seven specimens of *I. semicastaneus* (Kieffer), four specimens of *I. rufescens* (these last nine species identified by the first author), and one specimen each of five unidentified species. The nomenclature of aedeagus (Fig. 1) follows that of Johnson (1984).

Results

The aedeagus of each of the 17 studied species is distinguishable by: a) ratio of aedeagal lobe, digiti, aedeago-volsellar shaft and basal ring, b) number, shape and length of digital teeth. Among these species we recognise four different groups having a similar structure of aedeagus:

- a) 'flavicornis' type (Figs 2, 3, 4) (three species; see also Table 1): tip of the aedeagal lobe pointed, maximum width of aedeago-volsellar shaft near its base, aedeagus gradually narrowing, small digiti;
- b) 'rufescens' type (Figs 5, 6, 7), the most common among the 17 studied species (nine species): aedeagus clearly narrowing beyond digiti, maximum width of aedeago-volsellar shaft near the digiti, tip of the aedeagal lobe mostly rounded;
- c) 'semicastaneus' type (Figs 8, 9, 10) (two species): aedeagus with almost constant width, feebly narrowing beyond digiti, tip of the aedeagal lobe truncate;
- d) 'zonatus' type (Figs 11, 12, 13) (three species): tip of the aedeagal lobe truncate; this type of aedeagus is mainly characterised by two sclerotised strips in the middle of aedeagal lobe, differently from the other three groups, in which the aedeagal lobe is sclerotised at sides.

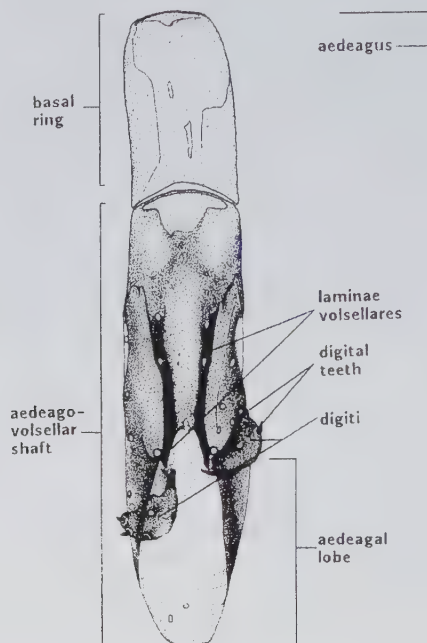
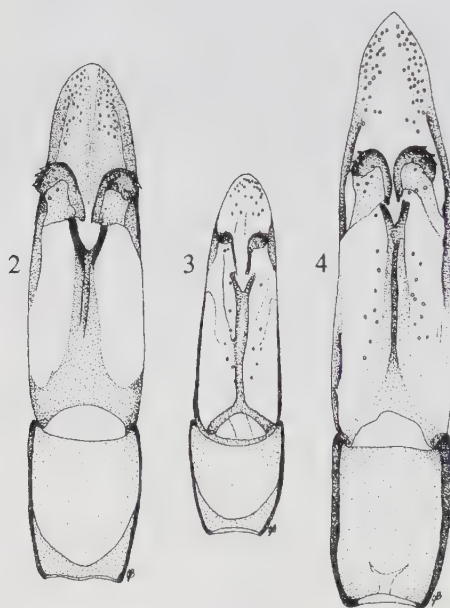


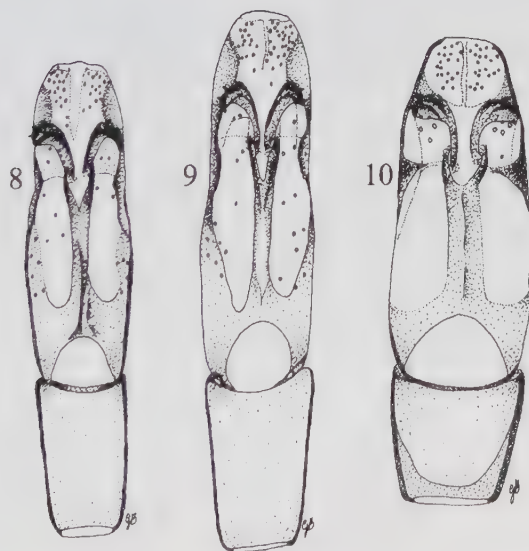
Figure 1 Male genitalia of a scelionid wasp, following the nomenclature of Johnson (1984) (after Polaszek & Kimani 1990)



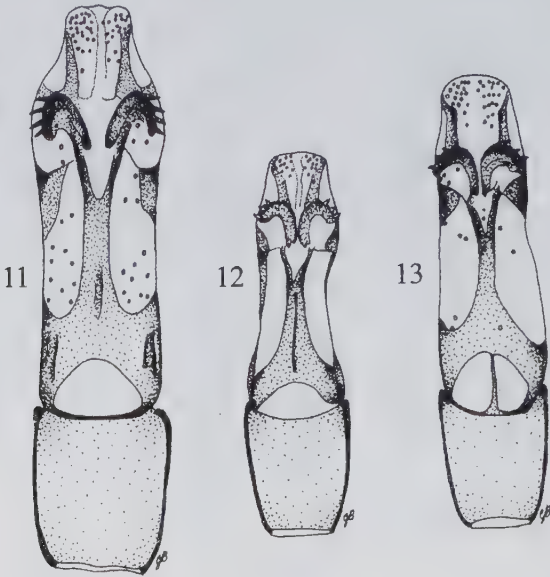
Figures 2–4 Aedeagi of the 'flavicornis' type: 2, *Idris flavicornis*; 3, *I. glabratus*; 4, *I. psammon*



Figures 5–7 Aedeagi of the 'rufescens' type: 5, *Idris rufescens*; 6, *I. nigroclavatus*; 7, *Idris* sp.5



Figures 8–10 Aedeagi of the 'semicastaneus' type: 8, *Idris semicastaneus*;
9, *I. semicastaneus*; 10, *I. priesneri*



Figures 11–13 Aedeagi of the ‘zonatus’ type: 11, *Idris* sp. 2; 12, *I. zonatus*; 13, *Idris* sp. 1

Table 1 Type of aedeagus and number of digital teeth in 17 Palaearctic species of *Idris* Foerster

Species	Type of aedeagus	Number of digital teeth	Species-group (Huggert, 1976)
<i>Idris glabratus</i> Huggert	‘flavicornis’ type	3	specie sola
<i>I. flavicornis</i> Foerster	‘flavicornis’ type	3	flavicornis-group
<i>I. psammon</i> Szabó		3	
<i>I. rufescens</i> (Kieffer)		2	rufescens-group
<i>I. aureonitens</i> Szabó	‘rufescens’ type	3–4	
<i>I. semiflavus</i> (Kieffer)		3	zonatus-group
<i>I. zonatus</i> (Kieffer)	‘zonatus’ type	3	
<i>I. semicastaneus</i> (Kieffer)	‘semicastaneus’ type	3	ater-group
<i>I. priesneri</i> Huggert		2	
<i>I. piceiventris</i> (Kieffer)		3	piceiventris-group
<i>I. meridionalis</i> Masner	‘rufescens’ type	3	
<i>I. nigroclavatus</i> (Kieffer)		3	
<i>Idris</i> sp. 1	‘zonatus’ type	3	-
<i>Idris</i> sp. 2	‘zonatus’ type	4	-
<i>Idris</i> sp. 3	‘rufescens’ type	2	-
<i>Idris</i> sp. 4	‘rufescens’ type	3	-
<i>Idris</i> sp. 5	‘rufescens’ type	2–3	-



Discussion

In this preliminary study, the morphology of the aedeagus in 17 studied Palearctic species of the genus *Idris* has shown interesting differences in the shape and could help to better characterise the species-groups of this genus. As shown in Table 1, the species included by Huggert (1979) in the same species-group have the same type of aedeagus, but its general shape should not be exclusive of just one group, as the presence of the 'rufescens' and 'flavicornis' types of aedeagus also in other groups seems to confirm.

It could be interesting to examine the male genitalia of as much as possible *Idris* species relating their features to other morphological characters.

Acknowledgements

We thanks Giusy Buglisi for all drawings.

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BIOLOGICAL AND MORPHOLOGICAL DIFFERENCES OF TWO CLOSELY RELATED SPECIES OF *SYNERGUS* FROM JAPAN

(HYMENOPTERA: CYNIPIDAE)

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Abstract – This work presents a study previous to the review of the Japanese species of *Synergus* Hartig. Biological studies have been conducted on *Synergus japonicus* Walker 1874. The ecological differences found by previous authors are supported by the morphological characters separating two species in the “*Synergus japonicus*” complex: *Synergus japonicus* Walker and *S. gifuensis* Ashmead.

Key words: Hymenoptera, Cynipidae, Synergini, Japan, *Synergus*, *S. japonicus*, *S. gifuensis*

Introduction

Among the Cynipidae, the genus *Synergus* is characterized, like other Synergini, by the loss of its cecidogenic abilities. For this reason, they are forced “inquilines” in galls of other cynipids. *Synergus* is connected with galls of members of the Cynipini tribe on different oak (*Quercus*) organs and rarely on chestnuts (*Castanea*). The cynipid inquilinism can be regarded as a kind of parasitism, and inquilines and gall inducing wasps are phylogenetically related. Since the biological relationship between the inquiline cynipids and the gall inducing cynipids only favours inquilines, Ronquist (1994) named this kind of relationship as agastoparasitism.

Monzen (1953) listed six species of *Synergus* from Japan, but the only species recorded after its description in ecological studies is *Synergus japonicus*. Masuda (1959) recognised two forms of *S. japonicus* on the basis of the differences in their life cycles and influence on the gall structure. Later, Abe (1990; 1992) extended the information about the existence of a complex of species.

Materials and Methods

Experimental series of *Synergus japonicus* ‘type A’ and *Synergus japonicus* ‘type B’ (according to Abe 1990) have been studied in ecological experiments (Abe 1990, 1992). Type specimens of *Synergus* described from Japan have also been studied (Pujade-Villar & Abe, *in prep.*).

SEM pictures of *Synergus* specimens from Abe’s collection were taken with gold coating.

We follow the current terminology of morphological structures given in Gibson (1985), Ronquist & Nordlander (1989), and Fergusson (1995). Abbreviations for fore wing venation follow Ronquist & Nordlander (1989).



Historical review

Masuda (1959) examined the biology of the *Synergus japonicus* complex developing in *Andricus mukaigawae* galls. Further studies with this complex were done in *Andricus kashiwaphilus* galls. According Abe (1990), *Synergus japonicus* has two ecological and biological forms: *S. japonicus* 'type A' and 'type B'.

The 'type A' is bivoltine or even with a possible third generation in summer (Abe 1990, 1992) and arrhenotokous. Adults of the first generation emerge from unisexual galls of *Andricus mukaigawae* and *A. kashiwaphilus* in May and the second generation emerge from bisexual galls of *Biorhiza weldi* (= *B. nawai*, synonym in Pujade-Villar, Ros-Farré & Melika 2002, *in press*) in June. Unisexual galls of *A. mukaigawae* are smaller when attacked by this inquiline (Abe 1990, 1992) and the inquiline-larval cells (Fig. 1a) are separated by a membranous wall.

The 'type B' is univoltine and also arrhenotokous. Adults emerge from unisexual galls of *Andricus mukaigawae* and *A. kashiwaphilus* in early June and females oviposit in newly produced host galls. Unisexual galls of *A. mukaigawae* are larger when attacked by this inquiline (Abe 1990, 1992) and include inquiline-larval cells (Fig. 1b) separated usually by a woody wall.

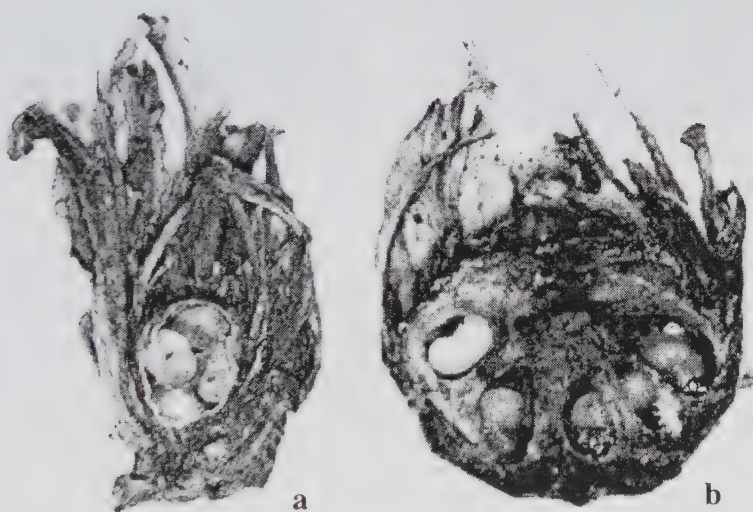


Figure 1 Longitudinal section of unisexual galls of *Andricus kashiwaphilus* Abe on *Quercus dentata* Thunberg with larvae of: a, *Synergus gifuensis*; b, *Synergus japonicus*

Discussion

After studies of *Synergus* species described from Japan, we have realized that "*S. japonicus* Type A" belongs to *Synergus gifuensis* Ashmead, 1904, and "*S. japonicus* Type B" is, in fact, *S. japonicus* Walker, 1874. Although the redescription of these species will be more detailed in the review of the Japanese *Synergus* species (Pujade-Villar & Abe, *in prep.*), we shall further stand out the main differences to recognize the females of these two species.

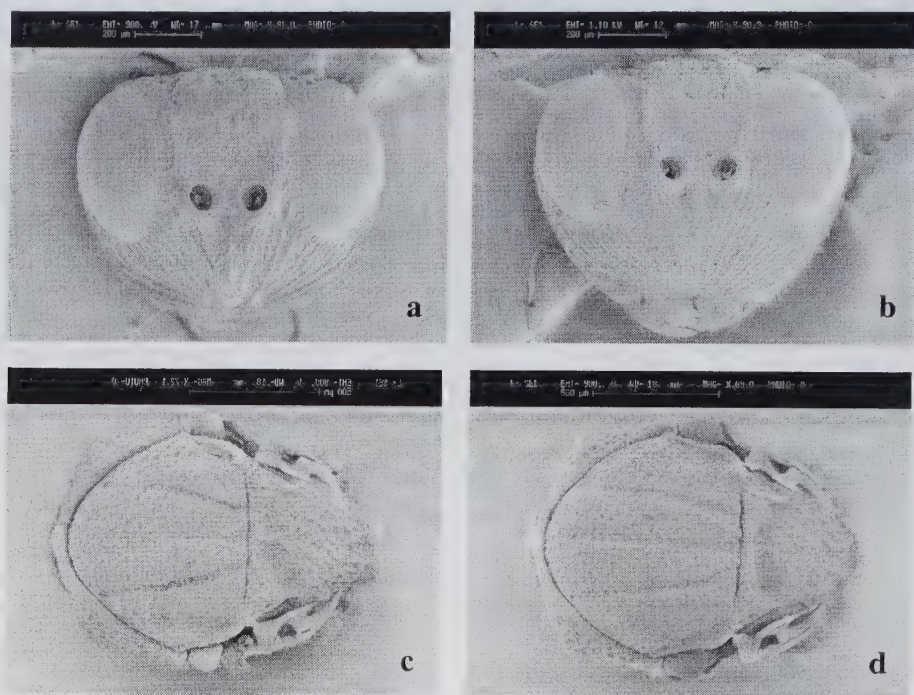


Figure 2 Head in front view and mesosoma in dorsal view of two closely related species of *Synergus* from Japan: a, c, *S. gifuensis*; b, d, *S. japonicus*

Females of *Synergus japonicus* and *S. gifuensis* are morphologically and chromatically very similar. Despite this, among other characters, *S. gifuensis* is less robust, with oval-shaped head in front view, with anastomosed carinae near the compound eye (Fig. 2a), the medial carina of the scutum is shorter (Fig. 1e), scutellar foveae are rugose (Fig. 2c); whereas *S. japonicus* is less robust, the head is more triangular in front view, and with a normal irradiating striae (Fig. 2b), the medial carina of the scutum is longer (Fig. 2d), scutellar foveae are smooth (Fig. 2d). The pronotum in *S. gifuensis* without basal defined carinae, which close a rugose area, while in *S. japonicus* the pronotum is more defined, has a medial carina. Finally, the superior distal form of the mesosoma is much more invaginated in *S. japonicus* than it is in *S. gifuensis*.

In conclusion, *Synergus japonicus* and *S. gifuensis*, biologically separated by the Japanese authors (see Introduction), show also morphological differences.

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PART 6

Biodiversity



BRACONIDAE SPECIES OF TURKISH AEGEAN REGION (HYMENOPTERA)

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Abstract – In this study, specimens of Braconidae were collected from a total 90 localities of the Aegean region in Spring, Summer and Autumn between the years 1996 and 1998 and were analysed. A total of 111 species belonging to six subfamilies (Agathidinae, Blacinae, Braconinae, Cheloninae, Microgastrinae and Rogadinae) were identified. All of the species are new record for Turkish Aegean region and of these, 11 are new records for Turkish Braconidae (Hymenoptera) fauna.

Key words: Aegean, Turkey, Agathidinae, Blacinae, Braconinae, Cheloninae, Microgastrinae, Rogadinae

Introduction

There are a few studies of Braconidae in Turkey. Several studies have involved Mediterranean and Marmara Regions (Beyarslan 1985, 1988, 1999; Beyarslan & Inanç 1990; Çetin & Beyarslan 2001; Inanç & Beyarslan 1990, 2001a, 2001b; Inanç 1997; Zettel & Beyarslan, 1992). This study deals with for the first time, Braconidae regarding Aegean region of Turkey.

Aegean region of Turkey is located in the west of Anatolia. It is surrounded by the regions of Midland Anatolia and Marmara, in the east and north, respectively. In the west of it, the Aegean Sea is placed. Its bounding is Taurus Mountains with Mediterranean Region of Turkey. The mountains which are not very high and have several plains between them, situated parallel to Aegean sea. In the midland parts the altitude of the mountains does not exceed 2000 m.

Aegean region has a Mediterranean climate in the littoral sides and plains. The vegetation is consisted of pine trees and maquis. Inland parts and higher areas have a continental climate, covered with grassland and sparse forests (Fig. 1).

Materials and Methods

Samples were collected from different habitat and altitudes of Aegean Region during three years (1996-1998).

The literature was used for taxonomical examination of materials. The specimens were identified according to (Fahringer 1934; Nixon 1968, 1970, 1986; Papp 1959, 1976, 1978, 1979, 1980, 1981, 1982, 1984a, 1984b, 1985, 1990, 1995; Shenefelt 1972, 1973; Simbolotti & Achterberg 1992, 1999; Tobias 1995).

Results

Out of a total 111 species belonging to six subfamilies (Agathidinae, Blacinae, Braconinae, Cheloninae, Microgastrinae and Rogadinae) were identified and listed below.

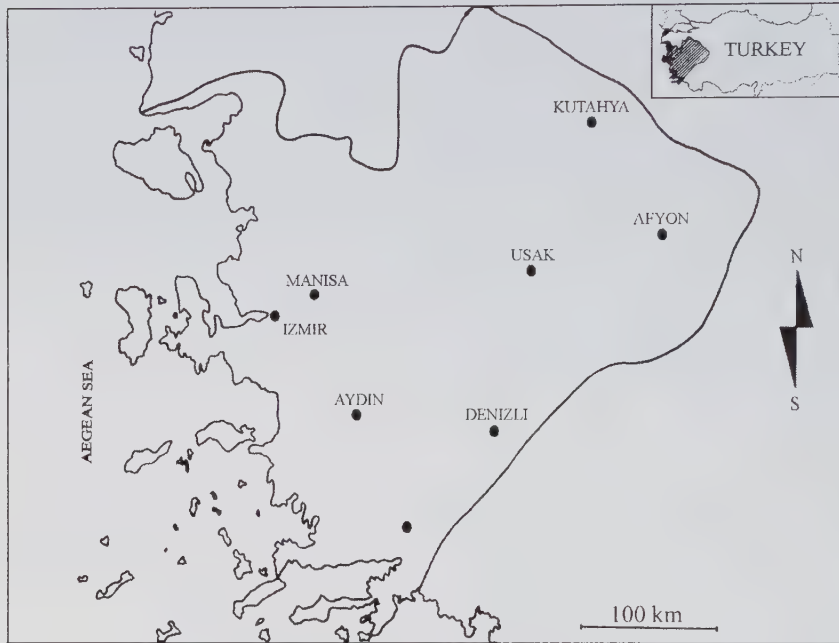


Figure 1 Turkey and Aegean Region

List of species

(* New records for Turkish Braconidae Fauna)

AGATHIDINAE

Agathis Latreille, 1804

- Agathis anglica* Marshall, 1885
- Agathis fuscipennis* (Zetterstedt, 1838)
- Agathis lugubris* (Foerster, 1862)
- Agathis malvacearum* Latreille, 1805
- Agathis montana* Shestakov, 1932
- Agathis nigra* Nees, 1814
- Agathis rufipalpis* Nees, 1814
- Agathis syngenesiae* Nees, 1814
- Agathis umbellatarum* Nees, 1814
- Agathis varipes* Thomson, 1895

Bassus Fabricius, 1804

- Bassus tumidulus* (Nees, 1814)

Disophrys Foerster, 1862

- Disophrys caesa* (Klug, 1890)

BLACINAE

Blacus Nees, 1818

Subgenus *Ganychorus* Haliday, 1835

- Blacus* (*G.*) *ruficornis* (Nees, 1812)*

BRACONINAE

Bracon Fabricius, 1804

Subgenus *Bracon* Fahringer, 1927

- Bracon* (*B.*) *fulvipes* (Nees, 1834)



- Bracon* (B.) *intercessor* (Nees, 1834)
Bracon (B.) *leptus* Marshall, 1897*
Bracon (B.) *longicollis* (Wesmael, 1838)*
Bracon (B.) *luteator* Spinola, 1808
Bracon (B.) *minutator* (Fabricius, 1798)
Bracon (B.) *pectoralis* (Wesmael, 1838)
Bracon (B.) *subglaber* Szépligeti, 1904*
Bracon (B.) *trucidator* (Marshall, 1888)

Subgenus *Glabrobracon* Fahringer, 1927

- Bracon* (G.) *anthracinus* (Nees, 1834)
Bracon (G.) *atrator* (Nees, 1834)
Bracon (G.) *fadiche* Beyarslan, 1996
Bracon (G.) *fumipennis* (Thomson, 1892)
Bracon (G.) *lividus* (Telenga, 1936)
Bracon (G.) *macrurus* (Thomson, 1892)
Bracon (G.) *obscurator* (Nees, 1812)
Bracon (G.) *pauris* Beyarslan, 1996
Bracon (G.) *picticornis* (Wesmael, 1838)
Bracon (G.) *popovi* Telenga, 1936
Bracon (G.) *variator* (Nees, 1812)

Subgenus *Habrobracon* Ashmead, 1900

- Bracon* (H.) *flavosignatus* (Tobias, 1957)*
Bracon (H.) *hebetor* (Say, 1836)
Bracon (H.) *nigricans* (Szépligeti, 1901)

Subgenus *Lucobracon* Fahringer, 1927

- Bracon* (L.) *erraticus* (Wesmael, 1838)
Bracon (L.) *hungaricus* (Szépligeti, 1896)
Bracon (L.) *nigriventris* (Wesmael, 1838)*

Subgenus *Rostrobracon* Tobias, 1957

- Bracon* (R.) *urinator* (Fabricius, 1798)

***Ceratobracon* Telenga, 1939**

- Ceratobracon* *stschegolevi* (Telenga, 1933)

***Glyptomorpha* Holmgren, 1868**

- Glyptomorpha* *pectoralis* (Brulle, 1832)

***Iphiaulax* Foerster, 1862**

- Iphiaulax* (I.) *jacopsoni* Shestakov, 1927

***Pigeria* Achterberg, 1985**

- Pigeria* *piger* (Wesmael, 1838)

***Pseudovipio* Szepligeti, 1896**

- Pseudovipio* *inscriptor* (Nees, 1834)

CHELONINAE

***Ascogaster* Wesmael, 1835**

- Ascogaster* *annularis* (Nees, 1813)*
Ascogaster *bidentulus* Wesmael, 1835*

***Chelonus* Jurine, 1801**

- Chelonus* *bidens* Tobias, 1976
Chelonus *canescens* Wesmael, 1835
Chelonus *inanitus* (Linnaeus, 1767)
Chelonus *microsomus* Tobias, 1964
Chelonus *oculator* (Panzer, 1779)
Chelonus *olgae* Kokujev, 1895*
Chelonus *scabrator* (Fabricius, 1793)
Chelonus *varimaculatus* Tobias, 1986

MICROGASTRINAE

***Apanteles* Foerster, 1862**

- Apanteles* *aragatzi* Tobias, 1976
Apanteles *ater* (Ratzeburg, 1852)
Apanteles *galleriae* Wilkinson, 1932
Apanteles *hemara* Nixon, 1965
Apanteles *myron* Nixon, 1973
Apanteles *obscurus* (Nees, 1834)

***Choeras* Mason, 1981**

- Choeras* *dorsalis* (Spinola, 1808)

***Cotesia* Cameron, 1891**

- Cotesia* *ancilla* (Nixon, 1974)
Cotesia *cupreus* (Lylé, 1925)
Cotesia *glomeratus* (Linnaeus, 1758)
Cotesia *kazak* (Telenga, 1949)
Cotesia *lineola* (Curtis, 1830)
Cotesia *nothus* (Marshall, 1885)
Cotesia *ofella* (Nixon, 1974)
Cotesia *plutellae* (Kurdjumov, 1912)
Cotesia *praepotens* (Haliday, 1834)
Cotesia *ruficrus* (Haliday, 1834)
Cotesia *saltatoria* (Balevski, 1980)
Cotesia *telangai* (Tobias, 1972)
Cotesia *tibialis* (Curtis, 1830)
Cotesia *zygaenarum* (Marshall, 1885)

***Dolichogenidea* Viereck, 1911**

- Dolichogenidea* *litae* (Nixon, 1972)
Dolichogenidea *longipalpis* (Reinhard, 1880)

Glyptapanteles Ashmead, 1905

- Glyptapanteles fulvipes* (Haliday, 1834)
Glyptapanteles lateralis (Haliday, 1834)
Glyptapanteles porthetriae (Muesebeck, 1928)

Iconella Mason, 1981

- Iconella albinervis* (Tobias, 1964)
Iconella lacteoides (Nixon, 1965)
Iconella merula (Reinhard, 1880)
Iconella myelonta (Wilkinson, 1937)

Sathon Mason, 1981

- Sathon falcatus* (Nees, 1834)

Illidops Mason, 1981

- Illidops naso* (Marshall, 1888)
Illidops urgo (Nixon, 1965)

Microgaster Latreille, 1804

- Microgaster alebion* Nixon, 1968
Microgaster globata (Linnaeus, 1758)
Microgaster stictica Ruthe, 1858
Microgaster subcompleta Nees, 1834

Microplitis Foerster, 1862

- Microplitis cebes* Nixon, 1970

Microplitis decens Tobias, 1964

- Microplitis decipiens* Prell, 1925
Microplitis deprimator (Fabricius, 1789)
Microplitis docilis Nixon, 1970
Microplitis fordi Nixon, 1970
Microplitis mandibularis Thomson, 1895
Microplitis marshallii Kokujev, 1897
Microplitis mediator (Haliday, 1834)
Microplitis scrophulariae Szépligeti, 1898
Microplitis spectabilis (Haliday, 1834)
Microplitis spinolae Nees, 1880
Microplitis tuberculifer (Wesmael, 1837)
Microplitis varipes Ruthe, 1860

ROGADINAE**Aleiodes Wesmael, 1838****Subgenus Neorhogas Szépligeti, 1906**

- Aleiodes* (N.) *bicolor* (Spinola, 1808)*
Aleiodes (N.) *circumscriptus* (Nees, 1834)
Aleiodes (N.) *dimidiatus* (Spinola, 1808)
Aleiodes (N.) *ductor* (Thunberg, 1822)*

Hygroplitis Thomson, 1895

- Hygroplitis russata* Haliday, 1834

Discussion

In order to establish the fauna of Turkish Braconidae (Hymenoptera), *Agathis varipes*, *Bracon* (G.) *fumipennis* in Mediterranean region and *Bracon* (B.) *luteator*, *Bracon* (B.) *trucidator*, *Bracon* (G.) *fadiche*, *Bracon* (G.) *lividus*, *Bracon* (G.) *picticornis*, *Microgaster globata*, *Microgaster stictica*, *Microgaster subcompleta*, *Microplitis deprimator*, *Microplitis docilis*, *Microplitis marshallii*, *Microplitis scrophulariae* in Marmara region. Except the new species and the species previously described, all of the species in this study are found both, in Mediterranean and Marmara regions.

The majority of the 111 species described in this study are distributed in the Palaearctic. The species mentioned above are their distributions are follows:

Holarctic: *Apanteles galleriae*, *Blacus* (G.) *ruficornis*, *Bracon* (B.) *pectoralis*, *Iconella merula*, *Pigiera piger*.

Palaearctic, Oriental, Australian: *Bracon* (R.) *urinator*, *Chelonus inanis*.

Palaearctic, Ethiopian: *Apanteles hemara*, *Ascogaster annularis*.

Holarctic, Oriental: *Sathon falcatus*.

Palaearctic, Oriental: *Cotesia glomeratus*, *Cotesia plutella*, *Microplitis mediator*.



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CHALCID WASPS FROM SOUTH GEORGIA (HYMENOPTERA: CHALCIDOIDEA)

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Abstract – Chalcid wasps were collected from South Georgia during 1994-2000. The chalcid fauna of this region is much more diverse than in Northern Caucasus, basically formed by widespread, common species: *Microterys sylvius* (Dalman), *M. hortulanus* Erdös, *M. lunatus* (Dalman), *Blastothrix longipennis* Howard (Encyrtidae); *Aphelinidae*: *Aphytis mytilaspidis* (Le Baron), *Coccophagus lycimnia* (Walker), *Ablerus atomon* (Walker) (Aphelinidae); *Pachyneuron muscarum* L. (Pteromalidae).

Key words: Southern Caucasus, Hymenoptera, Chalcidoidea, parasitoid

Introduction

Southern Georgia includes Small Caucasus (Adjara-Imereti, Trialeti, and Somkhiti mountain ranges, Akhaltsikhe hollow and Southern Georgia plateau). It is bordered with Turkey, Armenia and internal regions of Georgia and from the point of view of geography, biology and climate is a very interesting region, having a very specific floral and faunistic features. No chalcid fauna analysis was done in this region previously.

This is the first faunistic study on chalcid wasps of Southern Georgia which also includes some already published data (Nikolskaia & Yasnosh 1966, 1968; Trjapitzin 1968; Yasnosh 1983; Japoshvili 2000).

Results

The chalcid wasp fauna of Southern Georgia was studied during 1994-2000. We found about 48 species of chalcids belonging to 35 genera and 6 families. Only 15 species were listed from this region earlier (Nikolskaia & Yasnosh 1966, 1968; Trjapitzin 1968; Yasnosh 1983; Japoshvili 2000). From registered species 11 belong to the *Encyrtidae* family: *Anagyrus* sp., *Mahelencyrtus* sp., *Microterys sylvius* (Dalman), *M. hortulanus* Erdös, *M. lunatus* (Dalman), *Aphycus sumavicus* Hoffer, *Blastothrix longipennis* Howard, *Prionomitus mitratus* (Dalman), *Cheiloneurus claviger* (Thomson), *Sectiliclava cleone* (Walker), *Copidosoma floridanum* Ashmead; 11 to *Aphelinidae*: *Aphytis mytilaspidis* (Le Baron), *A. moldavicus* Jasnosh, *Coccophagus lycimnia* (Walker), *Ablerus atomon* (Walker), *Pteroptrix caucasicus* Jasnosh, *P. lauri* (Mercet), *P. bicolor* Howard, *Encarsia perniciosi* Tower, *Mesidiopsis subflavescens* (Westwood), *Aphelinus daucicola* Kurdjumov, *A. chaonia* Walker; 11 to *Pteromalidae*: *Metacolus azureus* Ratzeburg, *Pachyneuron muscarum* Linnaeus, *P. sp.*, *Dibrachys* sp., *Trichomalus* sp. aff. *pexatus* Walker, *Mesopolobus graminum* Hardh, *Cecidostiba geganius* Walker, *Habrocytus* sp. aff. *crassinervis* Thomson, *H. sp.*, *Pteromalus puparum* Linnaeus, *Dinarmus laticeps* Ashmead; 12 species to *Eulophidae*: *Phnigalio* sp.

(Eulophinae), *Elachertus nigrutilus* Zetterstedt (Elachertinae), *Chrysonotomyia formosa* Westwood, *Neochrysocharis* sp. aff. *immaculata* Kurdumov, *Omphale* sp. aff. *aetius* Walker (Entedontinae), *Tetrastichus* sp. aff. *biorizae* Szélnyi, *T. sp.* aff. *praecox* Graham, *T. phytomyzae* Kostjukov, *T. sp.* aff. *amethystinus* Ratzeburg, *T. conwentziae* Ferriere, *T. sp.* 1, *T. sp.* 2 (Tetrastichinae); 2 species to Torymidae: *Glyphomerus* sp. aff. *tibialis* Förster, *Torymus scoparii* Hoffmeyer; and one species to Mymaridae: *Limaenon* sp. Twenty three species are recorded for the Caucasus for the first time.

Our investigations showed that up to 1500-1700 m a.s.l. representatives of Encyrtidae and Aphelinidae families are dominated, while above 1700 m a.s.l. numbers of Pteromalidae and Eulophidae are increased. For 18 species hosts are known (Table 1), the rest of species were swept.

We defined the distribution of chalcids in Southern Georgia: approximately representatives of 5 genera had a very limited distribution, while species from 30 genera are widespread. The chalcid fauna of Southern Georgia is similar to that of temperate Southern Caucasus and the entire Palearctic Europe. We divided chalcids into the following zoogeographical groups:

Zoogeographical Group	Species
Cosmopolitan	<i>Pteromalus puparum</i> and <i>Coccophagus lycimnia</i>
Holarctic	<i>Copidosoma floridanum</i> , <i>Microterys sylvius</i> , <i>Blastothrix longipennis</i> , <i>Prionomitus mitratus</i> , <i>Aphytis mytilaspidis</i> , <i>Ablerus atomon</i> , and <i>Encarsia perniciosi</i>
Palearctic	<i>Microterys lunatus</i> , <i>Cheiloneurus claviger</i> , <i>Sectiliclava cleone</i> , <i>Mesidiopsis subflavescens</i> , <i>Aphytis chaonia</i> , and <i>Pachyneuron muscarum</i>
European	14 species
Caucasian-Turanian	<i>Microterys hortulanus</i> and <i>Aphytis daucicola</i>
Mediterranean	<i>Pteroptrix lauri</i>
Caucasian endemic	<i>Pteroptrix caucasicus</i>
Species with acritical propagation	<i>Glyphomerus</i> sp.aff. <i>tibialis</i> , <i>Dinarmus laticeps</i> , <i>Elachertus nigrutilus</i>

Conclusions

On the basis of our research of chalcid wasps of Southern Georgia we can conclude that:

- 23 species of chalcids are registered in the Georgian fauna for the first time;
- the chalcid complexes changed by altitude;
- most of species belong to the European complex.

Acknowledgements

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Table 1 Host-parasitoid relationships of Southern Georgia chalcids
(* – species registered by our investigation)

Chalcid Species	Host	Food plant
* <i>Microterys sylvius</i> (Dalman)	<i>Rhodococcus spirae</i> (Borchs)	<i>Spiraea</i>
* <i>M. hortulanus</i> Erdős	<i>Sphaerolecanium prunastri</i> Fonsc.	<i>Prunus domestica</i>
<i>M. lunatus</i> (Dalman)	<i>Physokermes piceae</i> (Schr.)	<i>Picea orientalis</i> Trjapitzin (1968)
<i>Aphycus sumavicus</i> Hoffer	<i>Phenacoccus montanus</i> Hadzh.	<i>Picea orientalis</i> Trjapitzin (1968)
* <i>Blastothrix longipennis</i> Howard	<i>Parthenolecanium corni</i> (Bouché)	<i>Thelicrania australis</i> , <i>Fraxinus</i> , <i>Crataegus</i>
* <i>Prionomitus mitratus</i> (Dalman)	<i>Psylla crataegi</i> Schr.	<i>Crataegus</i>
* <i>Cheiloneurus claviger</i> (Thomson)	<i>Parthenolecanium corni</i> (Bouché)	<i>Acer</i>
<i>Sectiliclava cleone</i> (Walker)	<i>Psylla mali</i> Schmidt	<i>Malus</i>
<i>Aphytis mytilaspidis</i> (Le Baron)	<i>Leucaspis pusilla</i> Löew	<i>Pinus</i> (Nikolskaia & Yasnosh 1968)
<i>A. moldavicus</i> Jasnosh	<i>Epidiaspis leperii</i> (Sign.)	(Nikolskaia & Yasnosh 1966)
<i>Coccophagus lycimnia</i> (Walker)	<i>Parthenolecanium corni</i> <i>Sphaerolecanium prunastri</i>	<i>Crataegus sp.</i> <i>Prunus</i> (Nikolskaia & Yasnosh 1968)
* <i>Ablerus atomon</i> (Walker)	<i>L. pusilla</i> Löew	<i>Pinus</i>
<i>Pteroptrix caucasicus</i> Jasnosh	<i>Quadraspidiotus ostreaformis</i> Curt.	<i>Malus domestica</i> , <i>Prunus</i> <i>domestica</i> (Nikolskaia & Yasnosh 1968)
<i>P. lauri</i> (Mercet)	<i>Quadraspidiotus armeniacus</i> Borchsenius, <i>Lepidosaphes ulmi</i> L.	(Nikolskaia & Yasnosh 1968)
<i>P. bicolor</i> (Howard)	<i>Diaspidiotus pyri</i> Licht. <i>D. perniciosus</i> Comst.	Yasnosh (1983)
<i>Encarsia perniciosi</i> Tower	<i>D. perniciosus</i> Comst., <i>L. ulmi</i> L.	(Nikolskaia & Yasnosh 1968)
<i>Mesidiopsis subflavescens</i> (Westwood)	<i>Aphidoidea</i>	<i>Corylus</i> (Nikolskaia & Yasnosh 1966, 1968)
<i>Pachyneuron muscarum</i> L.	<i>P. corni</i> (Bouché)	<i>Thelicrania australis</i>

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POLISH XORIDINES AND THEIR HOST ASSOCIATIONS (HYMENOPTERA: ICHNEUMONIDAE: XORIDINAE)

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Abstract – Results of field collecting and careful rearing with data on host relationships and/or habitat preferences of 23 species of xoridines (Hymenoptera: Ichneumonidae: Xoridinae) are presented.

Key words: Hymenoptera, Ichneumonidae, Xoridinae, host-parasitoid relationship, Boring beetle

Introduction

Parasitoids of the idiobiont ectoparasitoid subfamily Xoridinae (Ichneumonidae) are represented in Europe by at least 40 species, about 28 of which occur in Poland. Although specimens of xoridines are sometimes reared by entomologists working on wood boring beetles (such as Cerambycidae, Buprestidae, Scolytidae, Anobiidae, Melandryidae), usually the host's identity has been based on supposition (though often expressed as if certain). The paper presents results of field collecting and careful rearing of xoridines in Poland in the years 1994-2001, as well as some unpublished data found in Polish collections. The precise host data are presented only when the cocoon of the parasitoid was found in a determined larval gallery, with host remains. In the case of museum specimens, host associations are considered only when proved by attached cocoon and/or host remains. The dates and places of collecting are presented only for rare species or those new for Polish fauna.

Results

Data on host relationships and/or habitat preferences of 23 species are presented.

Odontocolon rufiventris (Holmgren, 1860)

A rare species in Poland, recorded mainly from mountain and submountain areas. Prefers deciduous and mixed forests. Reared without indication of host from lime branches *Tilia cordata* infested by the melandrids *Hypulus bifasciatus* (F.) and *Conopalpus testaceus* (Oliv.). Łużna EA-00, 23.i.1999 em.iii-iv, 3♂♂ leg. A. Trzeciak.

Odontocolon spinipes (Gravenhorst, 1829)

A species clearly associated with spruce forests, in Poland known from the natural range of norway spruce *Picea abies* from mountains and the north-eastern part of the country. Host are not identified but adults were reared from spruce stumps infested by various bark and wood boring beetles including *Rhagium inquisitor* (L.) (Cerambycidae) and *Ips typographus* (L.) (Ipidae).

***Odontocolon geniculatum* (Kriechbaumer, 1889)**

A species recorded from several localities, collected from May until July around dead or cut conifers (common fir *Abies alba*, scots pine *Pinus silvestris*).

***Odontocolon dentipes* (Gmelin, 1790)**

A common species associated with coniferous trees mainly with scots pine but also with common fir. Reared from the cerambycids *Arhopalus rusticus* (L.) on scots pine and *Anastrangalia dubia* (Scop.) on common fir. Pink-whitish cocoons are located in the wood in larval galleries of the host, usually several millimetres from the bark surface. There are probably two generations per year because adults were observed around host-infested stumps and trees from beginning of May until September with two peaks in May and August.

***Ischnoceros caligatus* (Gravenhorst, 1829)**

A very common polyphagous species (Fig. 1). Prefers coniferous and mixed forests. Characteristic boat shaped cocoons (Fig. 2) were found in galleries of cerambycids under the bark of: scots pine and norway spruce on *R. inquisitor*, larch *Larix* sp. on *Tetropium gabrieli* Weise, common fir on *Molorchus minor* (L.), oak *Quercus* sp. and black alder *Alnus glutinosa* on *Leiopus nebulosus* (L.), oak on *Rhagium mordax* (De Geer) and lime on *Oplosia fennica* (Payk.).

***Ischnoceros rusticus* (Geoffroy, 1785)**

A species associated with the cerambycid *Saperda carcharias* (L.), reared from poplar *Populus* sp. stumps infested by host larvae.

***Xorides hedwigi* Clément, 1938**

A very rare species. I have seen only one specimen from Poland (Fig. 3), reared from a cocoon found under the bark of lime in a larval gallery of the cerambycid *Mesosa curculionoides* (L.). 1♀ Wołów XS-18, 17.v.2000, leg. J. Hilszczański.

***Xorides praecatorius* (Fabricius, 1793)**

This is one of the most common and polyphagous xoridines. Prefers deciduous and mixed forests. Whitish or brownish cocoons are usually found under bark, although in one case a cocoon was found inside a twig of buckthorn *Frangula alnus* in a larval gallery of the cerambycid *Menesia bipunctata* Zoubk. *X. praecatorius* was recorded also as a parasitoid of the cerambycids *Phymatodes testaceus* (L.), *P. pusillus* (F.) and *P. alni* (L.) on oak, *L. nebulosus* on oak and alder, *Obrium cantharinum* (L.) on aspen *Populus tremula* (Fig. 4), *Leioderus collari* (Redt.) on sycamore *Acer pseudoplatanus*, and the buprestid *Agrilus viridis* (L.) on willow *Salix* sp. Although prefers hosts in deciduous trees *X. praecatorius* was found also on norway spruce as a parasitoid of *Molorchus minor*.

***Xorides indicatorius* (Latreille, 1806)**

A rare species (Fig. 5) associated with aspen. Dark or rarely light brown cocoons are found under the bark in larval galleries of the cerambycid *Saperda perforata* (Pall.) (Fig. 6). Adults emerge mostly in first half of May. Sękocin Las DC-97 1♂ 7.v.1996; 5♀♀ 1♂ 6-7.v.2000; 3♀♀ 2♂♂ 8.iv.2001, leg. J. Hilszczański.

***Xorides gravenhorstii* (Curtis, 1831)**

A species recorded a few times from Poland. Associated with deciduous trees. Reared as a parasitoid of *Molorchus umbellatarum* (Schreb.) (Cerambycidae) on apple tree *Malus* sp. and

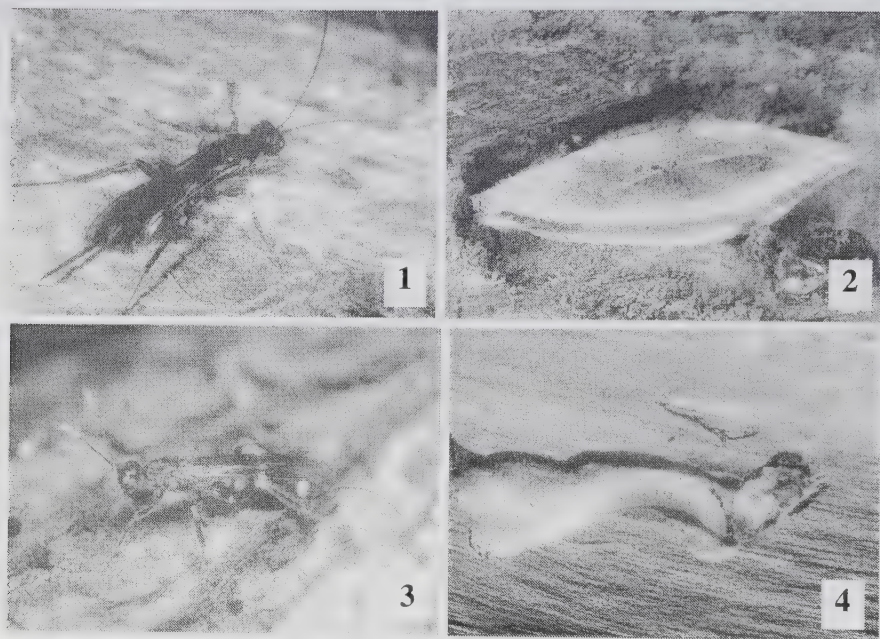
without indication of host from elm *Ulmus* sp. infested with *Scolytus multistriatus* (Marsh.) (Ipidae) and *Magdalis* sp. (Curculionidae).

***Xorides irrigator* (Fabricius, 1793)**

A common species inhabiting coniferous forests, mainly scots pine forests. Reared as a parasitoid of *R. inquisitor* and *Tetropium castaneum* (L.) on scots pine and *Obrium brunneum* (F.) on common fir.

***Xorides fuligator* (Thunberg, 1822)**

A species rarely collected in Poland. Inhabiting deciduous forests. Associated probably with cerambycids on oak. Biebrza Marshes National Park 1♀ vii-viii.1999, Kopciowe FE-01, yellow cup, leg. J. Hilszczański.



Figures 1–4 1, *Ischnoceros caligatus* (Grav.), female; 2, *Ischnoceros caligatus* (Grav.), cocoon with remains of larva of cerambycid *Rhagium inquisitor* L.; 3, *Xorides hedwigi* Clement, female; 4. *Xorides praecatorius* (F.), larva and remains of larva of cerambycid *Obrium cantharinum* (L.) (photo by C. Bystrowski)

***Xorides niger* (Pfeffer, 1913)**

Associated with conifers. Most frequently reared from the cerambycid *M. minor* on scots pine and common fir. One specimen was reared from a cocoon found in a larval gallery of *Acanthocinus griseus* (F.) (Cerambycidae) on scots pine.

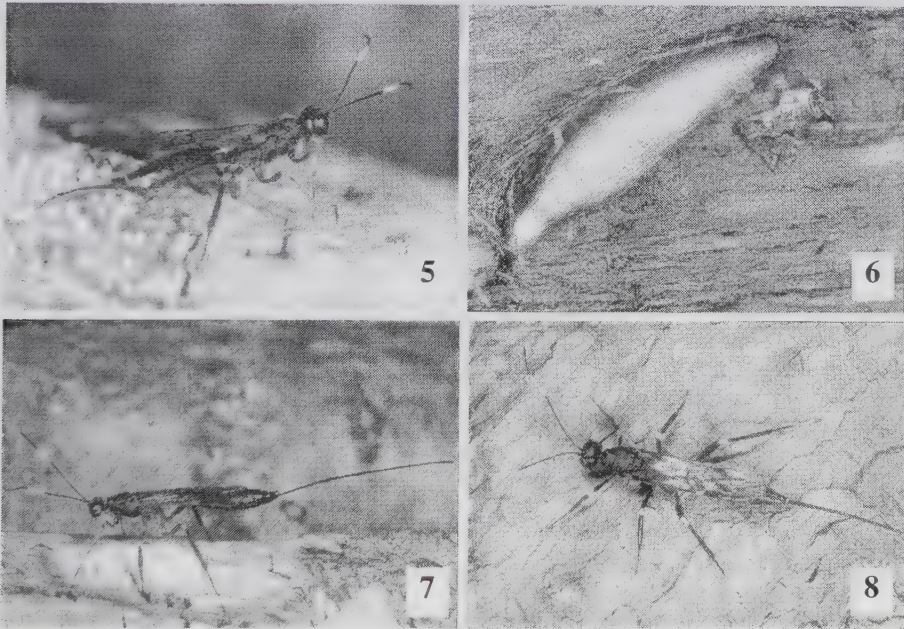
***Xorides csikii* Clément, 1938**

A rare species, known in Poland only from two specimens. 1♀ Rogów DC-24, 1.v.1968, leg. J. Sawoniewicz; 1♂ Ostrów Mazowiecka ED-55, yellow cup 22.v.1995 leg. J. Hilszczański. In

England the species was reared from an oak twig (Shaw, *pers. comm*), and probably in Poland is also associated with this tree species. The species is new to the Polish fauna.

***Xorides alpestris* (Habermehl, 1903)**

This species was recorded by Šedivý (1958) as a parasitoid of *Necydalis maior* L., and this cerambycid has been mentioned as the only host of *X. alpestris* by many later authors. In Poland *X. alpestris* (Fig. 7) is not rare and inhabits deciduous and mixed forest, infesting larvae of cerambycids living in old dead wood of birch *Betula* sp. and black alder on *Leptura quadrifasciata* L., hazel *Corylus avellana* and mountain ash *Sorbus aucuparia* on *Leptura aethiops* Poda and common fir on *Anastrangalia dubia* (Scop.). Dark or light brown cocoons are located deep in the wood. The size of cocoons depends on sex; female cocoons are longer and enable the adult with straightened ovipositor to find enough room. This phenomenon is seen also in other xoridines, but is especially spectacular in species with a long female ovipositor.



Figures 5–8 5, *Xorides indicatorius* (F.), female (photo by C. Bystrowski);
6, *Xorides indicatorius* (F.), cocoon and remains of larva of cerambycid *Saperda perforata* (Pall.)
(photo by W. Janiszewski); 7, *Xorides alpestris* (Haberm.), female (photo by C. Bystrowski);
8, *Xorides sepulchralis* (Holm.), female (photo by C. Bystrowski)

***Xorides sepulchralis* (Holmgren, 1860)**

A species (Fig. 8) associated with cerambycids of the genus *Xylotrechus*. In Poland found in larval galleries of *X. rusticus* (L.) on aspen and poplar. The dark brown cocoon is often situated in the end of exit hole of the host's larva from the sapwood, so that one end of the cocoon is visible when the bark is removed.

***Xorides filiformis* (Gravenhorst, 1829)**

A common species, in Poland often reared from the cerambycid *P. testaceus* infesting oak.

***Xorides brachylabis* (Kriechbaumer, 1889)**

A common species strongly associated with cerambycids of the genus *Tetropium*. During the present study reared from cocoons found in larval galleries of *T. castaneum* on norway spruce and scots pine and from *T. gabrieli* on larch.

***Xorides ater* (Gravenhorst, 1829)**

A rare species, only one specimen reared from a cocoon found under dead scots pine bark with attached remains of lepturine larva, probably *Corymbia rubra* (L.) (Cerambycidae). 1♀ Ziemiećice CA-38, 2.v.1998, leg. J. Hilszczański.

***Xorides depressus* (Holmgren, 1860)**

A rarely collected species, recorded by Herve (1937) as a parasitoid of *Phaenops cyanea* F. (Buprestidae) and later by Šedivý (1958) as parasitoid of *Nothorina punctata* F. (Cerambycidae) developing in the same habitat. In the years 1997-2001 during research on *P. cyanea* thousands of beetle specimens were reared from scots pine bark from several localities in Poland. In spite of the abundance of the host only two specimens of *X. depressus* were reared. 2♀♀ Gostynin CD-91, 6.ii.2001 em. iii. leg. A. Sowińska and W. Janiszewski.

***Xorides ephialtoides* (Kriechbaumer, 1882)**

A species associated with buprestids of the genus *Dicerca* infesting deciduous trees. In Poland reared from *Dicerca berolinensis* (Herbst) on beech *Fagus silvatica* (Hilszczański 2000).

***Xorides flavotibialis* Hilszczański, 2000 and *Xorides ilignus* Hilszczański, 2000**

These recently described species are known so far only from the deciduous mixed forest of Biebrza Marshes National Park (Hilszczański 2000).

In addition to the above listed species the following are also recorded from Poland, (verified by checking existing specimens): *Odontocolon punctulatum* (Thom.), *O. quercinum* (Thom.), *O. thomsoni* Clem., *O. appendiculatum* (Grav.), *Xorides rufipes* (Grav.).

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ICHNEUMONIDAE SPECIES OF THE TURKISH AEGEAN REGION

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Abstract – Ichneumonidae were collected from 32 localities of the Aegean region, Turkey during spring, summer and autumn in 1996-1998. A list of 42 ichneumonid species from eight subfamilies (Pimplinae, Cryptinae, Banchinae, Phrudinae, Cremastinae, Campopleginae, Anomaloninae, Ichneumoninae) and short zoogeographical notes to them are given.

Key words: Pimplinae, Cryptinae, Banchinae, Phrudinae, Cremastinae, Campopleginae, Anomaloninae, Ichneumoninae

Introduction

The Ichneumonidae fauna of Turkey is not well known. Kolarov (1995) catalogue includes only 383 species. Some recent studies are contributed to this list (Kolarov *et al.* 1997a, 1997b 1999 & Özbek *et al.* 2000). Since Turkey has an interesting geographical location, with different climatic conditions and high floristic diversity, a rich Ichneumonidae fauna is expected. In the study, The majority of the material in this study was collected from the Aegean Region of Turkey (Fig. 1). Forty two ichneumonid species from subfamilies Pimplinae, Cryptinae, Banchinae, Phrudinae, Cremastinae, Campopleginae, Anomaloninae, Ichneumoninae were identified. Eight of them are new records for the Turkish Ichneumonidae fauna (marked by asterisk in the text). General distribution data for each species, mainly after Kasparyan (1981) and some short zoogeographical notes are given also.

Results

A list of 42 ichneumonid species from the Aegean Region of Turkey is given below.

Pimplinae

1. *Exeristes robotator* (Fabricius, 1793)

Denizli-Cardak, 28.6.1998, 2♂♂; -Kale, 27.6.1998, 1♀, 1♂; Mugla-Gokova-Kemertur, 26.6.1998, 2♀♀, 2♂♂.

Distribution: Palearctic.

2. *Exeristes arundinis* (Kriechbaumer, 1887)*

Denizli-Cardak, 28.6.1998, 4♀♀.

Distribution: Middle and South Europe, Latvia, Kazakhstan, Middle Asia, Mongolia and Pacific Cost of Russia.

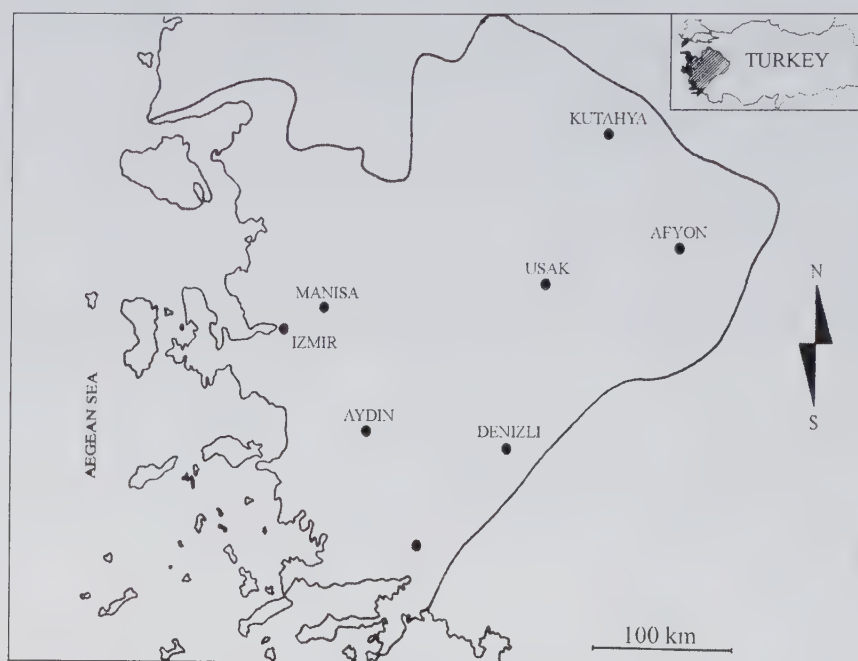


Figure 1 Turkey and the Aegean Region

3. *Endromopoda arundinator* (Fabricius, 1804)

İzmir-Oglananasi, 24.6.1998, 2♂♂; Manisa-Kula, 30.6.1998, 1♂.

Distribution: Europe, Algeria and Mongolia.

4. *Endromopoda detrita* (Holmgren, 1860)

Afyon-Dinar-Kazanpinar, 28.06.1998, 1♂; Denizli-Kale, 27.6.1998, 1♀; İzmir-Karaburun-Baliklio, 23.6.1998, 2♀♀, 1♂.

Distribution: Europe, Asia Minor, Caucasus, Middle Asia, Russia (Sakhalin and Kamchatka) and North America.

5. *Scambus nigricans* (Thomson, 1877)

Afyon-Serinhisar-Salavatli, 19.9.1996, 5♀♀, 1♂; Denizli-Buldan-Kadikoy, 19.9.1996, 1♀.

Distribution: Europe, Caucasus, Kazakhstan and Middle Asia.

6. *Scambus foliae* (Cushman, 1938)*

Manisa-Kula, 30.6.1998, 1♂.

Distribution: Austria, Romania, Bulgaria and Russia (Komi and Sakhalin Island).

7. *Ephialtes manifestator* (Linnaeus, 1759)

Denizli-Cardak, 28.6.1998, 1♀; -Kale, 27.6.1998, 5♀♀; Kutahya-Gediz-Murat dagi-Sobaalani, 28.7.1997, 1♂; Manisa-Kula, 30.6.1998, 2♀♀; Usak-Ortakoy, 30.6.1998, 9♀♀.

Distribution: Europe, Caucasus and Tadzhikistan.

8. *Zaglyptus varipes* (Gravenhorst, 1829)

Denizli-Cardak, 28.6.1998, 1♂.

Distribution: Holarctic.

9. *Schizopyga podagrica* Gravenhorst, 1829*

Aydin-Kocarli-Cincin, 18.09.1996, 2♀♀.

Distribution: Palaearctic.

10. *Acrodactyla madida* Haliday, 1839

Denizli-Cardak, 28.6.1998, 1♀; -Kale, 27.6.1998, 5♀♀; Kutahya-Gediz-Murat dagi-Sobaalani, 28.7.1997, 1♂; Usak-Ortakoy, 30.6.1998, 9♀♀.

Distribution: Europe and Armenia.

11. *Itopectis maculator* (Fabricius, 1775)

Afyon-Bolvadin-Kapakli, 29.6.1998, 1♀; -Sincanli-Akoren, 26.7.1997, 1♀; Balikesir-Burhaniye-Pelit, 22.6.1998, 1♂; Denizli-Tavas-Tekkekoy, 27.6.1998, 1♀; Mugla-Marmaris-Degirmenyani, 26.6.1998, 2♀♀, 1♂; -Yaras, 27.6.1998, 1♂.

Distribution: Canarian Islands, Europe, Turkey, North Africa and introduced to North America.

12. *Pimpla spuria* Gravenhorst, 1829

Afyon-Bayat-Koroglu, 29.06.1998, 1♂; -Sincanli-Akoren, 26.7.1997, 1♀; Denizli-Tavas-Tekkekoy, 27.6.1998, 1♀; Manisa-Gordes-Gunesli, 23.7.1997, 1♀; Mugla-Marmaris-Degirmenyani, 26.6.1998, 1♀; Usak-Banaz, 27.7.1997, 1♀.

Distribution: Europe, Turkey, Kazakhstan, Middle Asia, Altay and Iran.

13. *Perithorus scurra* (Panzer, 1804)

Afyon-Sincanli-Akoren, 26.7.1997, 1♀; Usak-Banaz, 27.7.1997, 1♀.

Distribution: Holarctic.

Cryptinae

14. *Lysibia nanus* (Gravenhorst, 1829)

Aydin-Germencik-Morali, 24.6.1998, 1♂.

Distribution: Europe and ?Japan.

15. *Aclastus micator* (Gravenhorst, 1807)

Afyon-Sincanli-Akoren, 26.7.1997, 1♀; Mugla-Gokova-Kemertur, 26.6.1998, 2♀♀, 2♂♂; -Marmaris-Degirmenyani, 26.6.1998, 2♀♀, 1♂; -Yaras, 27.6.1998, 1♂.

Distribution: Western Europe.

16. *Aclastus solutus* (Thomson, 1884)

Afyon-Sincanli-Akoren, 26.7.1997, 1♀; Mugla-Marmaris-Degirmenyani, 26.6.1998, 2♀♀, 1♂; -Yaras, 27.6.1998, 1♂.

Distribution: Europe.

17. *Dichrogaster aestivalis* (Gravenhorst, 1829)

Afyon-Evciler-Körkuyu, 28.6.1998, 1♀; -Sincanli-Karacaoren, 27.7.1997, 2♀♀, 3♂♂; Denizli-Tavas-Tekkekoy, 30.7.1997, 2♂♂.

Distribution: Europe and Caucasus.

18. *Gelis rufipes* (Bridgman, 1883)

Afyon-Evciler-Korkuyu, 28.6.1998, 1♀; Denizli-Zeytinkoy-Bagbasi, 30.7.1997, 1♀.

Distribution: Europe.

19. *Mesoleptus scrutator* (Haliday, 1839)*

Afyon-İhsaniye-Yenicekoy, 26.7.1997, 1♀, 1♂; Denizli-Civril-Kocayaka, 29.7.1997, 4♀♀; -Tavas-Tekkekoy, 27.6.1998, 1♀; İzmir-Menemen-Karakoyun, 2.8.1997, 1♂; Usak-Banaz, 27.7.1997, 1♀, 3♂♂.

Distribution: Europe.

20. *Gambus carnifex* (Gravenhorst, 1829)

Afyon-İhsaniye-Yenicekoy, 26.7.1997, 1♀, 1♂; Denizli-Civril-Kocayaka, 29.7.1997, 4♀♀; -Tavas-Tekkekoy, 27.6.1998, 1♀.

Distribution: Europe.

21. *Cryptus triguttatus* (Gravenhorst, 1829)

Afyon-Sincanlı-Akoren, 26.7.1997, 1♀; Mugla-Marmaris-Degirmenyani, 26.6.1998, 2♀♀, 1♂; -Yaras, 27.6.1998, 1♂.

Distribution: Europe and Middle Asia.

22. *Ischnus agitator* (Olivier, 1792)

Afyon-İhsaniye-Yenicekoy, 26.7.1997, 1♀, 1♂; Denizli-Civril-Kocayaka, 29.7.1997, 4♀♀; İzmir-Menemen-Karakoyun, 2.8.1997, 1♂; Usak-Banaz, 27.7.1997, 1♀, 3♂♂.

Distribution: Europe.

Banchinae**23. *Lissonata flavovariegata* (Lucas, 1849)**

İzmir-Karaburun-Baliklioia, 23.06.1998, 6♂♂.

Distribution: South Europe, North Africa, Turkey and Iran.

24. *Lissonata mediterranea* Seyrig, 1927

Afyon-Dinar-Kazanpinar, 28.06.1998, 4♀♀.

Distribution: South Europe.

Phuridinae**25. *Phaestacoenitus caucasicus* Kasparyan, 1983***

Afyon-Dinar-Kazanpinar, 28.06.1998, 1♂; Denizli-Tavas-Tekkekoy, 27.06.1998, 1♂.

Distribution: Azerbaijan and Georgia.

26. *Phaestacoenitus niger nitidus* Kasparyan, 1983*

Denizli-Tavas-Tekkekoy, 27.06.1998, 1♀.

Distribution: North Caucasus.

Cremastinae**27. *Pristomerus armatus* (Lucas, 1849)**

Mugla-Datca-Emecik, 26.06.1998, 6♀♀.



Distribution: Europe, North Africa, Turkey, Georgia, Armenia, Kazakhstan, Uzbekistan, Turkmenia, Kirgizia and Russia (Siberia).

28. *Pristomerus horribilis* Narolsky, 1987*

Afyon-Emirdag-Koruca, 29.6.1998, 2♂♂.

Distribution: Germany, Switzerland, Bulgaria and Ukraine.

29. *Temelucha arenosa* Szépligeti, 1899

Afyon-Dinar-Kazanpinar, 28.06.1998, 6♀♀; -Emirdag-Koruca, 29.6.1998, 5♀♀.

Distribution: Western Europe, Yugoslavia, Bulgaria and Turkey.

30. *Temelucha decorata* (Gravenhorst, 1829)

Afyon-Dinar-Kazanpinar, 28.06.1998, 1♂; Denizli-Cardak, 28.06.1998, 1♀, 1♂.

Distribution: Greenland, Western Europe, Balkan Peninsula, Romania, Moldavia, Turkey and Azerbaijan.

31. *Temelucha lucida* (Szépligeti, 1899)*

Afyon-Dinar-Kazanpinar, 28.06.1998, 1♀.

Distribution: Czech Republic, Hungary, Bulgaria and Moldavia.

32. *Temelucha observator* Aubert, 1966

Afyon-Dinar-Kazanpinar, 28.06.1998, 1♂; Denizli-Cardak, 28.06.1998, 1♂; Mugla-Milas-Camici, 24.06.1998, 1♀, 2♂♂.

Distribution: Morocco, Tunisia, Turkey, Egypt, Israel, Romania and Ukraine (Crimea).

Campopleginae

33. *Casinarina ischnogaster* Thomson, 1887

Afyon-Sincanlı-Akoren, 26.7.1997, 1♀; Mugla-Marmaris-Degirmenyani, 26.6.1998, 1♀; Usak- Banaz, 27.7.1997, 1♀.

Distribution: Europe.

34. *Charops cantator* (De Geer, 1778)

Afyon-Bayat-Koroglu, 29.06.1998, 3♀♀, 1♂; Mugla-Yaras, 27.06.1998, 2♀♀.

Distribution: Europe, Caucasus and Russia (behind Baikal Lake Region).

35. *Bathyplectes carinatus* Horstmann, 1974

İzmir-Menemen-Karakoyun, 2.8.1997, 1♂; Mugla-Gokova-Kemertur, 26.6.1998, 1♀; Usak-Banaz, 27.7.1997, 1♀, 3♂♂.

Distribution: Middle Europe, Bulgaria and Turkey.

36. *Chromoplex picticollis* (Thomson, 1887)

İzmir-Karaburun-Balikliova, 23.06.1998, 2♀♀; Mugla-Milas-Korucuk, 24.06.1998, 3♀♀, 1♂.

Distribution: France, Bosnia-Herzegovina, Greece, Bulgaria, Turkey, Egypt and Israel.

37. *Camponotus mitis* (Holmgren, 1860)

Afyon-Sincanlı-Akoren, 26.7.1997, 1♀; Mugla-Marmaris-Degirmenyani, 26.6.1998, 1♀; Usak- Banaz, 27.7.1997, 1♀.

Distribution: Europe.

38. *Alsima orbitale* (Gravenhorst, 1829)

Afyon-Sincanlı-Karacaören, 27.7.1997, 1♂; Mugla-Gokova-Kemertur, 26.6.1998, 1♀; -Milas-Korucuk, 24.06.1998, 2♀♀; Usak-Banaz, 27.7.1997, 1♀, 3♂♂.

Distribution: Europe, Caucasus and Russia (Siberia, around Baikal Lake).

Anomaloninae**39. *Anomalon cruentatum* (Geoffroy, 1785)**

Afyon-Bayat-Koroglu, 29.06.1998, 4♀♀, 3♂♂; Mugla-Yaras, 27.06.1998, 2♀♀, 2♂♂.

Distribution: Central, South and East Europe, Kazakhstan, Middle Asia and Russia (Southern West Siberia).

40. *Trichomma enecator* (Rossi, 1790)

Afyon-Bayat-Koroglu, 29.06.1998, 1♀.

Distribution: Palaearctic.

41. *Agryphon flexorium* (Thunberg, 1822)

Afyon-Bayat-Koroglu, 29.06.1998, 1♀.

Distribution: Palaearctic.

Ichneumoninae**42. *Diadromus collaris* (Gravenhorst, 1829)**

Aydın-Germencik-Morali, 24.06.1998, 5♀♀, 4♂♂; Mugla-Yaras, 27.06.1998, 2♀♀, 2♂♂.

Distribution: Europe, Canarian Islands, South West and Middle Asia.

Discussion

The listed species can be divided into the next groups according to their zoogeographical distribution:

Holarctic region: 3 species, *Endromopoda detrita*, *Zaglyptus varipes* and *Perithous scurra*.

Palaearctic region: 7 species, *Exeristes arundinis*, *E. roborator*, *Scambus foliae*, *Schizopyga podagrica*, *Lysibia nanus*, *Trichomma enecator* and *Agryphon flexorium*.

Euro-sibirian: 4 species, *Pristomerus armatus*, *Charops cantator*, *Alsima orbitalis* and *Anomalon cruentatum*.

Twenty two species belong to European. Several of them are distributed in Europe, Asia Minor and some of them in the Caucasus: *Ephialtes manifestator*, *Acrodactyla madida*, *Itopectis maculator*, *Aclastus micator*, *A. solutus*, *Dichrogaster aestivalis*, *Gelis rufipes*, *Mesoleptus scrutator*, *Gambrus cornifex*, *Ischnus agitator*, *Pristomerus horribilis*, *Temelucha arenosa*, *T. decorata*, *T. lucida*, *Casinaria ishnogaster*, *Bathyplectes carinatus*, *Campoletis mitis*. Other species besides Europe are distributed also in Kazakhstan, Middle Asia and rarely in Mongolia: *Endromopoda arundinator*, *Pimpla spuria*, *Scambus nigricans*, *Cryptus triguttatus* and *Diadromus collaris*.

Lissonata flavovariegata is an Irano-turanian species.

Three species, *Lissonata mediterranea*, *Temelucha observator* and *Chromoplex picticollis* belong to the Mediterranean complex.



Two endemic Caucasian species, *Phaestacoenitus caucasicus* and *Phaestacoenitus niger nitidus*, recently described (Kasparyan 1983), were also found in the Aegean region.

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HYMENOPTERA PARASITICA COMMUNITIES OF AGROECOSYSTEM TYPES IN NORTHEAST GERMANY

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Abstract – This study was carried out in the biosphere reserve Schorfheide-Chorin in northeast Germany. A total of 4 cereals fields, 4 set asides, and 2 grasslands were investigated. Ground photo-eclectors ($n = 6$ /study site) were used to obtain quantitative population data of Hymenoptera Parasitica. In total 23 families of Hymenoptera Parasitica and 74 Chalcidoidea genera were collected during the spring and early summer of 1995. Cereals fields were distinguished from other agroecosystems by the number of taxa and their respective abundances. Number and mean abundances of Hymenoptera Parasitica and Chalcidoidea genera did not vary among set asides in spite of different successional stages. Initial stages of set asides and grassland already produced high Chalcidoidea genera numbers and abundances.

Key words: cereal fields, set aside, grassland, ground photo-eclector

Introduction

Hymenoptera Parasitica are becoming important organisms for studying the effects of land use management. Results can be used to design strategies for natural biological control. Past studies have shown that Hymenoptera Parasitica benefit from uncultivated land in agricultural landscapes (e.g. Altieri *et al.* 1993; Barbosa 1998; Ferro & McNeil 1998; Nentwig *et al.* 1998). This study focuses on the effects of different types of agroecosystems on abundances and distribution patterns of Hymenoptera Parasitica.

Materials and Methods

The study was carried out in the development zone of the biosphere reserve Schorfheide-Chorin located approximately 75 km northeast of Berlin, Germany, during the spring and early summer of 1995 (27.03.–20.07.1995). Study sites included cereal fields ($n = 4$), set asides ($n = 4$), and grasslands ($n = 2$) which comprise the main agricultural land use systems (Table 1). Cereal fields differed mainly by their farming methods. The land use type “set aside” included study sites of different successional stages. Two grasslands were distinguished by their cultivation type and agricultural management (Table 1).

The Hymenoptera Parasitica were collected by ground-photoeclectors ($n = 6$ /study site) (Funke 1971; Roth 1985) enclosing 1 m² of vegetation and soil. Using ground photo-eclectors, results can be presented as quantitative data (Individuals/m²). The Hymenoptera Parasitica other than Chalcidoidea were determined at family level. The Chalcidoidea were specified at genus level

and the genus *Aprostocetus*, Eulophidae at subgenera level, respectively. Comparisons of family and genera abundances were limited to the group of dominant taxa comprising 85% of the total individuals collected (Engelmann 1978). Statistical analysis was based on mean abundance (median), Spearman rank correlation (r), Kruskal-Wallis-Anova (H-test) and Mann-Whitney U-test (U-test). For statistical reasons, conclusions of U-test were taken into consideration by a threshold $p < 0,01$ (Sokal & Rohlf 1995). Statistical analysis were carried out by Statistica (StatSoft 1999).

Table 1 Characterization of study sites

land use type	study site	farming method	cultivation type
cereal field	A 1	conventional	winter rye
cereal field	A 2	conventional	winter barley
cereal field	A 6	conventional	winter rye
cereal field	A 9	bio-dynamic	winter rye
set aside	B 4	(conventional)	set aside (1 st yr)
set aside	B 12	(conventional)	set aside (1 st yr)
set aside	B 10	(conventional)	set aside (5 th yr)
set aside	B 11	(conventional)	set aside (> 10 yrs)
grassland	G 8	bio-dynamic	hay meadow (1 st yr)
grassland	G 3	conventional	pasture (sheep-run) (> 10 yrs)

Results

In total, 23 families of Hymenoptera Parasitica and 74 Chalcidoidea genera were collected. Number of families varied between 13 and 19 at individual study site. The lowest number of families was found at cereal fields A 1, A 2, and A 6. A 9 produced the same number of families as B 4. B 12 and G 3 contained the highest number of families (Table 2).

Table 2 Median, results of H-Test of dominant Hymenoptera Parasitica families ($df = 9$, $n = 55$; $p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$; total individuals (n), numbers of Hymenoptera Parasitica families (N), and median of Hymenoptera Parasitica (total median) for each study site; families collected in single individuals (median = 0) are noted as "+")

	cereal field				set aside				grassland		H-Test	total
	A 1	A 2	A 9	A 6	B 4	B 12	B 10	B 11	G 8	G 3	($df = 9$, $n = 55$)	ind.
Scelionidae	12	4	31	60.5	62.5	85	59.5	83	46	46.5	0.0000***	3158
Pteromalidae	3	2.5	3.5	3	32.5	12.5	24	14.5	15	5	0.0000***	753
Braconidae	2	5.5	3	4	12.5	20	9.5	6	7	4.5	0.0045**	560
Eulophidae	+	2	2	7	15	10	12	12	17	13.5	0.0009***	549
Platygastridae	3	18.5	+	2.5	6	3	9.5	4	18	2	0.0267*	420
Ceraphronidae	1.5	2.5	7.5	2	3.5	8.5	8	7.5	14	5.5	0.0073**	362
Mymaridae	+	+	1.5	3	4.5	5.5	3	12	6	1	0.0009***	345
Ichneumonidae	1	2.5	0.5	6.5	10.5	8.5	6	4.5	18	4	0.0000***	342
total n	163	354	388	601	1071	1110	1109	964	943	689		7392
total N	14	13	16	14	16	19	18	15	18	19		23
total median	26	56	61.5	84	171	174.5	184.5	151.5	166	109.5	0.0000***	

Twenty-two out of 74 genera of Chalcidoidea appertained to the group of dominant genera. The total number of genera at individual study sites ranged from 11 (A 1) to 36 (B 10). Thus none of the study sites held more than half of the total number of genera found. The number of genera was lowest at the cereal fields. In addition, many genera found at the set asides or grasslands were not identified from some cereal field but all genera found from the cereal fields were collected either at the set asides or at the grasslands. A 9, a bio-dynamically cultivated cereal field that was a set aside in a previous year, held the most genera (22 genera) within the land use type cereal field (Table 3).

Table 3 Median, results of H-Test of dominant Chalcidoidea genera (df = 9, n = 55; $p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$; total individuals (n), numbers of Chalcidoidea genera (N), and median of Hymenoptera Parasitica (total median) for each study site; genera collected in single individuals (median = 0) are noted as “+”)

		cereal field				set aside			grassland		H-test	total	
		A 1	A 2	A 9	A 6	B 4	B 12	B 10	B 11	G 8	G 3	(df = 9, n = 55)	ind.
<i>Aprostocetus</i>	Euloph.		+		5.5	12	8	3.5	3.5	7	6	0.0002***	292
<i>Anaphes</i>	Mym.			+	2	1	3	2	9	2	+	0.0030**	180
<i>Tetramesa</i>	Eurytom.			1		1	1.5	9	1.5	5	1	0.0001***	163
<i>Callitula</i>	Pterom.	1.5	+	+	0.5	7	0.5	3	1	4	1.5	0.0002***	135
<i>Eurytoma</i>	Eurytom.			+		+	2	7.5	1		0.5	0.0010**	129
<i>Homoporus</i>	Pterom.		+	+	+	1	+	4	2.5	1		0.0023**	70
<i>Stenomalina</i>	Pterom.	1		0.5		+	0.5	2	1.5	+	+	0.0369*	67
<i>Neochrysocharis</i>	Euloph.							2	4			0.0000***	59
<i>Cea</i>	Pterom.			+	+	3.5	1	1.5	+	+		0.0001***	58
<i>Trichomalus</i>	Pterom.	+	+	+	+	+	2	+	4.5	+		0.0007***	52
<i>Cyrtogaster</i>	Pterom.	0.5			+	2.5	2.5	0.5	+	1	+	0.0009***	48
<i>Polynema</i>	Mym.			+		+	1.5		1.5	2	+	0.0001***	47
<i>Gonatocerus</i>	Mym.	+	+	+		+	+	1	+	1	+	0.4527	46
<i>Meraporus</i>	Pterom.			+	+	2.5		+	+	+		0.0003***	45
<i>Halticoptera</i>	Pterom.	+				3.5	+	+		+	+	0.0035**	43
<i>Anagrus</i>	Mym.	+	+			0.5				+	+	0.1024	43
<i>Pediobius</i>	Euloph.	+	+	+	1	+	+	2.5		+		0.0036**	37
<i>Eupelmus</i>	Eupelm.			+		1	+	1	1		+	0.0052**	35
<i>Bruchophagus</i>	Eurytom.			+			2	0.5	1	+		0.0146*	32
<i>Mesopolobus</i>	Pterom.			+	+	+	+	4			+	0.0849	30
<i>Gastrancistrus</i>	Pterom.						0.5		+		0.5	0.0224*	26
<i>Necremnus</i>	Euloph.				+	+	+	+		1		0.0840	26
total n		25	45	71	57	309	281	382	345	255	183		1952
total N		11	14	22	15	27	31	36	32	31	32		74
total median		4	6	13	15.5	53	36.5	54.5	59	67	27	0.0000***	

The abundance of the total Hymenoptera Parasitica differed (H-test; df = 9, $p = 0.0000$) among all study sites. Mean Hymenoptera Parasitica abundances were lower in cereal fields (median = 26–84 Ind./m²) than in set asides or grasslands (median = 109.5–184.5 Ind./m²). When comparing individual study sites to each other, abundances of cereal fields A 1, A 2, and A 9 differed to the set aside sites (U-test; $p < 0.01$). Differences between cereal fields and grasslands were restricted

to A 1 and G 3 (U-test; $p < 0.01$), though G 3 produced the lowest median (median = 109.5 Ind./m²) of study sites other than cereal fields. Within cereal fields, the mean Hymenoptera Parasitica abundance of A 6 (median = 84 Ind./m²) was the highest. The Hymenoptera Parasitica median of A 2, A 9, and A 6 was greater by two times than median of A 1, although differences (U-test; $p < 0.01$) of abundances were confined to A 1 and A 9. All set asides produced about the same mean abundances of Hymenoptera Parasitica ranging from 151.5 Ind./m² to 184.5 Ind./m². B 4, a study site that was set aside in a previous year and G 8, an initial grassland, produced mean abundances more than twice as high as cereal fields under cultivation. No significant differences were found for both grasslands (Fig. 1, Table 2, Table 4).

Table 4 U-test of total Hymenoptera Parasitica individuals (absolute results of U-test are shown at the right of table, only significant results are shown; results within statistical thresholds are at the left ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$); shaded fields indicate the comparison of study sites within the same land use type)

		cereal field				set aside				grassland	
		A 1	A 2	A 9	A 6	B 4	B 12	B 10	B 11	G 8	G 3
cereal field	A 1			0.004	0.011	0.004	0.004	0.004	0.004	0.020	0.004
	A 2					0.006	0.004	0.004	0.004	0.020	
	A 9	**				0.006	0.004	0.004	0.004	0.020	
	A 6	*									
set aside	B 4	**	**	**							
	B 12	**	**	**							0.037
	B 10	**	**	**							
	B 11	**	**	**							
grass-land	G 8	*	*	*							
	G 3	**					*				

Differences of Chalcidoidea abundances were observed among all study sites (H-test; $df = 9$, $p < 0.0000$). Like the result totals from the Hymenoptera Parasitica, A 1 produced the lowest median (median = 4 Ind./m²). In contrast to Hymenoptera Parasitica, the highest median was found at G 8 (67 Ind./m²). The highest mean abundance of cereal fields (A 6: median = 15.5 Ind./m²) attained, at maximum, approximately half of the mean abundances of study sites others than cereal fields. Chalcidoidea abundances at each set aside area differed in comparison to A 1, A 2, and A 9 (U-test; $p < 0.01$). Differences in abundance between study sites of cereal fields and grasslands were restricted to G 3 and A 2 (U-test; $p < 0.01$). Similar to the results of total Hymenoptera Parasitica abundances, there were no relevant differences of Chalcidoidea abundances among study sites of set asides or grasslands as well as between study sites of both land use types. Initial set aside B 4 and initial grassland G 8 produced more than two times the mean abundances than any other cereal field (Fig. 2, Table 3, Table 5).

The Chalcidoidea constituted approximately a quarter of the total Hymenoptera Parasitica individuals (Table 2, Table 3). Total abundance patterns of Hymenoptera Parasitica (Fig. 1) were similar to the Chalcidoidea abundance pattern (Fig. 2). The interrelations of Hymenoptera Parasitica medians with Chalcidoidea medians were strongly correlated ($r = 0.81$, $p < 0.01$).

Table 5 U-test of total Chalcidoidea individuals (absolute results of U-test are shown at the right of table, only significant results are shown; results within statistical thresholds are at the left ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$); shaded fields indicate the comparison of study sites within same land use type)

		cereal field				set aside				grassland	
		A 1	A 2	A 9	A 6	B 4	B 12	B 10	B 11	G 8	G 3
cereal field	A 1			0.013	0.019	0.004	0.004	0.004	0.004	0.020	0.031
	A 2					0.004	0.004	0.004	0.004	0.020	0.004
	A 9	*				0.005	0.006	0.004	0.004	0.020	
	A 6	*				0.019	0.025	0.011	0.011		
set aside	B 4	**	**	**	*						
	B 12	**	**	**	*						
	B 10	**	**	**	*						
	B 11	**	**	**	*						
grass-land	G 8	*	*	*							
	G 3	*	**								

All dominant families were collected on each study site. Except for Platygastriidae, significant differences of individual family abundances were found (H-test, $df = 9$, $p < 0.01$). The most dominant family was the Scelionidae, which made up 43% of the total number of individuals. The Scelionidae reached higher proportions in cereal fields A 1, A 9 und A 6. The Platygastriidae were the dominant family at cereal field A 2. This family has been the only one that attained the maximum median on a cultivated field (A 2). Three families of Chalcidoidea belonged to the group of dominant families. In general, they were collected in low individual numbers from cereals fields. Maximum mean abundance of the Pteromalidae was achieved by B 4. G 8 produced the maximum median of the Eulophidae, and B 11 of Mymaridae, respectively (Fig. 1, Table 2).

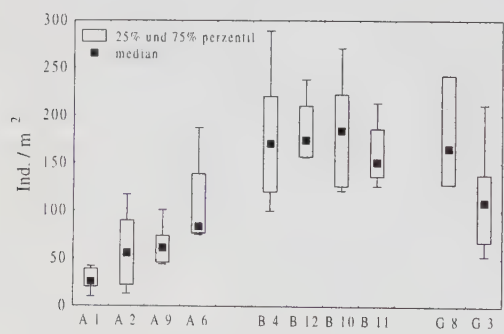


Figure 1 Abundances (Ind./m²) of total Hymenoptera Parasitica at study sites

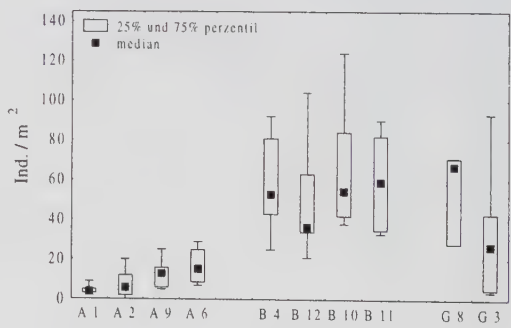


Figure 2 Abundances (Ind./m²) of total Chalcidoidea at study sites

Abundances of the dominant Chalcidoidea genera varied significantly (H-test, $df = 9$, $p < 0.01$) with the exception of the genera *Gonatocerus*, *Anagrus*, *Mesopolobus*, and *Necremnus*. However, all 4 genera mentioned did not exceed a total number of 50 individuals and ranked in the group of

the dominant taxa because of high individual numbers in single ground photo-electors. A maximum median for all genera was reached at set asides with the exception of *Polynema* and *Gastrancistrus*. Ten genera out of the dominant ones pertained to Pteromalidae. *Aprostocetus* achieved the highest number of individuals (Fig. 1, Table 3). Most individuals from this genera belonged to subgenus *Aprostocetus*.

Discussion

The presented results underline conclusions of past studies. For example, Altieri *et al.* (1993); Ferro & McNeil (1998); Marino & Landis (1996); Nentwig *et al.* (1998); Thies & Tschardtke (1999); Landis *et al.* (2000) have all demonstrated that diversity and individual numbers of Hymenoptera Parasitica were enhanced by agroecosystems other than cultivated fields. On the other hand, Pankanin-Franczyk (1987) did not find any effects by landscape structures on Aphidiinae, Braconidae inhabiting rye fields. Thus, there is need for an accurate analysis of the response of each single taxa to different agroecosystem types. This study carried out on various agroecosystems on a small spatial scale, enables a comparison and an assessment of agroecosystems values for communities or single taxa of Hymenoptera Parasitica and Chalcidoidea. Information on community ecology (Hawkins 1994) or on preferred agroecosystems of specific parasitoid taxa, expand the knowledge on their distribution patterns and biology. Information on habitat preferences of taxa acting as pest antagonists benefit strategies for natural biological control as it is outlined by Ehler (1994); Barbosa (1998).

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PART 7

Biology, ecology and Behaviour



HOST SPECTRA OF PALAEARCTIC MICROGASTRINES (HYMENOPTERA: BRACONIDAE: MICROGASTRINAE)

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Abstract – The dominant host-parasite relations of palaearctic microgastrines with Lepidoptera are considered. The following trend is found: the larger microgastrine genera have the wider spectrae of host-parasite relations. The pattern of host-parasite relations of the subfamily Microgastrinae shows the greatest similarity to these patterns of subfamilies Euphorinae and Rogadinae. The role of hyperparasites (certain Chalcidoidea and Ichneumonidae) in the population dynamics of Braconidae is shown on the example of the gypsy moth (*Lymantria dispar* L.) parasite complex.

Key words: Braconidae, Microgastrinae, Palaearctic, parasite, hyperparasite, host-parasite relations, Lepidoptera, *Lymantria dispar*

Introduction

Microgastrinae is one of the largest subfamilies of braconid wasps. According to Mason (1981) only the genus *Apanteles* sensu lato counts from 5 to 10 thousand species all over the world. Only in Great Britain more than 250 species of microgastrines have been recorded until now (Shaw & Huddleston 1991). Currently more than 600 species and 25 genera are noted for the Palaearctic. More than 90% of the Palaearctic microgastrines belong to 6 largest genera: *Apanteles*, *Cotesia*, *Dolichogenidea*, *Glyptapanteles*, *Microgaster*, *Microplitis*. Host-parasite relations are more or less known only for less than 50% of palaearctic species of Microgastrinae. Hosts are known only for 20-40% of species that belong to the mentioned large genera.

It is typical for Microgastrinae to parasitize caterpillars of Lepidoptera as koinobiotical solitary, more rarely as group parasites (I agree with the argumentation of Viktorov (1976), that the use of the term "parasitoids" for parasitic hymenopterans is scientifically unjustified). Reports indicating them from beetle larvae should be revised, and indications from spider cocoons are certainly erroneous. The error is possibly due to the fact that the joint web cocoons of certain species of *Cotesia* and *Glyptapanteles* are somewhat similar to the cocoons of spiders. Host-parasite relations of Microgastrinae are revealed for less than a half of the known Palaearctic species. In large genera the percentage of species for which hosts have been discovered reaches from 20 to 40. At the species level microgastrines are mostly oligophages (often quite narrow). Monophagous behavior is more likely to occur at the population level. Records indicating the extended oligophagous behaviour or, even more, polyphagous behaviour need to be checked.

Results and Discussion

Out of 37 subfamilies of Braconidae (as understood by Belokobyl'skij & Tobias 1998) of the World fauna 22 (almost 60%) are linked with lepidopterans. Out of this number, 17 subfamilies

(more than 77%), including Microgastrinae, are specialized parasites of Lepidoptera. For comparison, it could be noted that only 8 subfamilies of Braconidae have established host-parasite relationships with such a large order as Coleoptera and only 3 subfamilies (Brachistinae, Cenocoelinae, Helconinae) are the specialized parasites of beetles. For the other orders of insects linked with braconids the figures are even lower. Hence, lepidopterans present a group of hosts, which tremendously favoured a splash in the evolution of braconids. A revealing feature for the majority of the subfamilies of Braconidae linked with lepidopterans (20 out of 22) is their cosmopolitan distribution.

Amongst braconid parasites of Lepidoptera in the Palaearctic Microgastrinae have the broadest spectrum of hosts (44 families and 17 superfamilies). Further far behind are the subfamilies Euphorinae (26), Rogadinae (23), Cheloninae (19), Braconinae (18), Exothecinae (17). These data are evident on the table 1. There is a clear trend indicating that larger (that is, more rich in species) genera have a broader array of hosts (see Table 2). The maximum number of host families (24) is recorded for the largest genus *Cotesia* (above 150 species in the Palaearctic). Further in descending order we have: *Dolichogenidea* (22 host families falling to 150 species), of the genus *Apanteles* (18 families falling to about 100 species), *Microgaster* (15 families for 70 species), *Glyptapanteles* (10 families for 40 species), *Microplitis* (6 families for 100 species), *Diolcogaster* and *Pholetesor* (each at 5 families of hosts for 20-25 species of parasites). For each of the genera *Illidops*, *Protapanteles*, *Choeras*, numbering from 15 to 30 species, 4 host families have been recorded. For the genus *Iconella* (about 25 species in the Palaearctic) hosts are coming only from 2 families of lepidopterans. For the remaining genera that are less rich in species, relations are traced with 1-2 families of hosts.

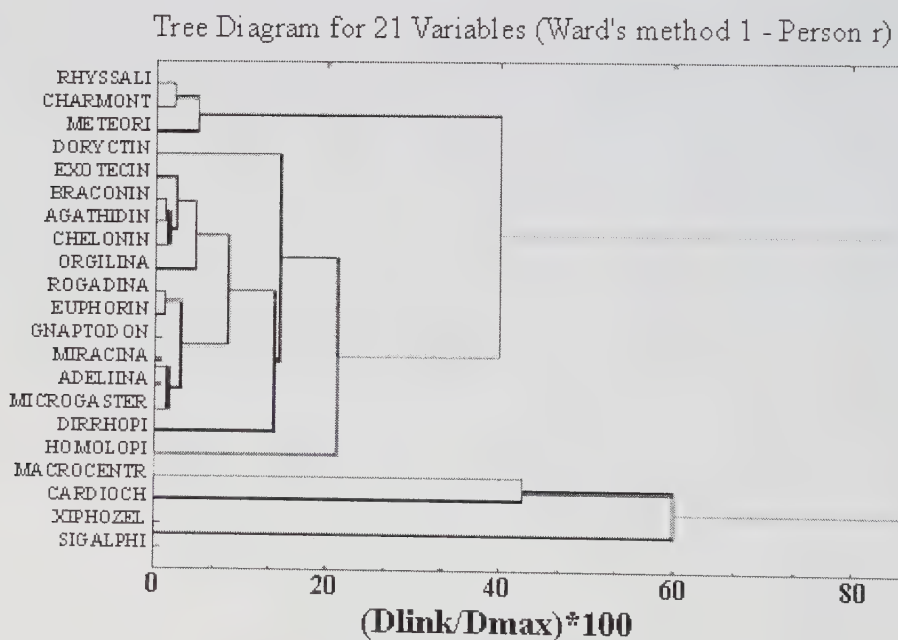


Figure 1 Cluster analysis of Braconidae subfamilies



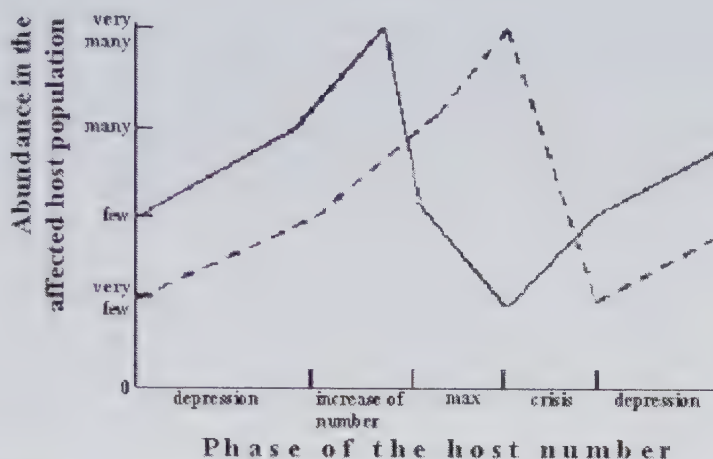


Figure 2 Dynamics of abundance of braconids parasites of the gypsy moth (*Lymantria dispar* L.) under various phases of the host number (for South Ukraine) (---- microgastrines, parasites of early-instar caterpillars; — braconids, parasites of middle and late-instar caterpillars)

In respect to host-parasite relations the subfamily Microgastrinae shows the greatest similarity to the subfamilies Euphorinae and Rogadinae. (Table 1). Numbers 0 to 3 in the table 1 indicate the degree of the linkage of braconids of various subfamilies to certain lepidopteran families: 0 – no links revealed; 1 – link not significant; 2 – link significant; 3 – link most significant; ? – link doubtful. A statistical analysis of the table data have been made. The considerable similarity of host-parasite relations of microgastrines, euphorines and rogadines is pointed out by the relatively high value of the Sorensen-Czekanovski coefficient (calculated according to Pesenko 1982). This similarity coefficient for Microgastrinae and Euphorinae totals 0.25; for Microgastrinae and Rogadinae – 0.22; and for Euphorinae and Rogadinae – 0.27. This is much more than the similarity coefficients calculated for these groups and accounting for the other subfamilies. The similar pattern of host-parasite relations of Microgastrinae, Euphorinae and Rogadinae is pointed out by the results of cluster as well (see Fig. 1). An explanation to such similarity can be given taking into consideration the ecological specifics of Microgastrinae, Euphorinae and Rogadinae. Representatives of these groups very often belong to a common complex of parasites. However, they differ according to their functional significance. Let us take as an example the well-studied complex of entomophages of the gypsy moth (*Lymantria dispar* L.) in Ukraine. Amongst braconids this complex is composed by the representatives of Microgastrinae belonging primarily to the genera *Cotesia* and *Glyptapanteles*, euphorine species of the genus *Meteorus* and rogadines of the genus *Aleiodes*. Braconids of other subfamilies are absent from this complex. Microgastrines-parasites of the gypsy moth, compared to species of *Meteorus* and *Aleiodes* have smaller dimensions (2.5 – 3.5 mm against 4.0 – 6.0 mm), and consequently have weaker flying abilities. At the same time microgastrines turn out to be quite competitive. In spring they appear earlier than other braconids and lay eggs primarily into early-instar caterpillars (I or II). Hence, using the gypsy moth they produce 2 generations before the end of the season. *Meteorus* spp. parasitize middle-instar caterpillars (III or IV), while *Aleiodes* spp. parasitize middle and late-instar caterpillars (IV or V). Thus, using the gypsy moth they usually produce only 1 generation

annually. There is no doubt that the relatively close link of the parasite to the age group of the host weakens the competition between various species of entomophages.

Table 1 Number of lepidopteran families linked with various subfamilies of Braconidae in Palaearctic (0 – no link revealed; 1 – link is not significant; 2 – link is significant; 3 – link is most significant; ? – link is doubtful)

LEPIDOPTERA	Rhyssalinae	Doryctinae	Exothecinae	Rogadinae	Braconinae	Gnaptodontinae	Euphorinae	Meteorideinae	MACrocentrinae	Xiphozelinae	Homolobinae	Charmontinae	Orgilinae	Sigalphinae	Agathidinae	Cheloninae	Cardiophilinae	Microgastrinae	Dirrhopinae	Miracinae	Adelinae	# of subfamilies
Acrolepiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	2
Arctiidae	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2
Argyrestidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	2	0	0	0	4
Bucculatricidae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Choreutidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Coleophoridae	0	1	1	0	2	0	1	0	1	0	0	0	3	0	3	1	0	3	0	0	0	9
Cosmopterigidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Cossidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Crambidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Drepanidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Elachistidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Endromidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Epermeniidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Eriocraniidae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Galleriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Gelechiidae	2	0	2	1	3	0	1	2	2	0	0	3	2	0	3	2	0	3	0	0	0	12
Geometridae	0	0	0	3	0	0	3	0	1	0	3	0	0	0	1	1	0	3	0	0	0	7
Gracillariidae	0	0	3	0	2	0	0	0	0	0	0	0	2	0	1	0	0	3	2	3	3	8
Heliozelidae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hepialidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Incurvariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Lasiocampidae	0	0	0	3	1	0	3	0	0	0	0	0	0	0	0	1	0	3	0	0	0	5
Limacodidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lithosiidae	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
Lycaenidae	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	3	0	0	0	5
Lymantriidae	0	0	0	3	?	0	3	0	?	0	0	0	0	0	0	0	0	3	0	0	0	5
Lyonetiidae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Momphidae	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	2	0	2	0	0	0	6
Nepticulidae	0	0	1	0	1	3	0	0	0	0	0	0	0	0	0	0	0	2	2	3	3	7
Noctuidae	0	0	0	3	1	0	3	0	3	3	2	1	0	3	1	2	0	3	0	0	0	11
Nolidae	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Notodontidae	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
Nymphalidae	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	3	0	0	0	4
Oecophoridae	1	0	0	1	1	0	1	0	2	0	1	2	1	0	2	3	0	3	0	0	0	11
Orneodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1
Papilionidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

LEPIDOPTERA	Rhyssalinae	Doryctinae	Exothecinae	Rogadinae	Braconinae	Gnaptodontinae	Euphorinae	Meteorideinae	MACROcentrinae	Xiphozelinae	Homolobinae	Charmontinae	Orgilinae	Sigalphinae	Agathidinae	Cheloninae	Cardiophilinae	Microgastrinae	Dirrhopinae	Miracinae	Adelinae	# of subfamilies
Phycitidae	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	2	0	3	0	0	0	8
Pieridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	2
Plutellidae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	3
Psychidae	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	1	2	0	0	7
Pterophoridae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	3
Pyralidae	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2	3	0	0	0	6
Pyraustidae	0	0	1	1	1	0	2	0	1	0	1	0	0	0	2	2	0	3	0	0	0	9
Saturniidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Satyridae	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
Scythrididae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Sesiidae	0	1	0	0	3	0	0	0	1	0	0	0	0	0	1	2	0	1	0	0	0	6
Sphingidae	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2
Tetheidae	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	3
Thaumetopoeidae	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
Tineidae	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	3	0	0	0	5
Tischeriidae	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Tortricidae	2	2	3	2	3	0	3	1	3	0	0	3	1	0	3	3	0	3	0	0	0	13
Yponomeutidae	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	2	0	3	0	0	0	6
Zygaenidae	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	4
# of families	4	3	17	23	18	1	26	2	15	1	4	5	8	1	17	19	1	44	3	2	2	

It should be mentioned that the relations between braconids in the complex of parasites of the gypsy moth are greatly influenced by hyperparasites (many Chalcidoidea and Ichneumonidae of the subfamilies Gelinae and Mesochorinae). In the spring and early summer the hyperparasites in the affected population of the host multiply in numbers rapidly, using braconid parasites of early and middle-instar caterpillars. This results in a later suppression of numbers of braconids parasitizing in middle and late-instar caterpillars. The activity of hyperparasites explains the difference in the dynamics and abundance of these two ecologically contrasting groups of braconids: on one side the parasites of early-instar caterpillars, on the other those of late-instar caterpillars (Fig. 2). Parasites of middle and late-instar caterpillars are more abundant under periods of low host numbers (depression phase and phase of increasing numbers). In the phase of the maximum numbers of the host and at the beginning of the crisis the number of the braconid parasites of middle and late-instar caterpillars drops sharply. They are suppressed by hyperparasites. It is very likely that the braconids of *Aleiodes* start to pupate not within exposed cocoons but within mumified caterpillars in order to avoid being affected by hyperparasites.

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Table 2 Number of lepidopteran families linked with various genera of Microgastrinae in Palaearctic

Microgastrinae		Lepidoptera (Hosts)
Genus	Number of species in the Palaearctic	Number of families
<i>Cotesia</i>	about 150	24
<i>Dolichogenidea</i>	150	22
<i>Apanteles</i>	about 100	18
<i>Microplitis</i>	100	6
<i>Microgaster</i>	70	5
<i>Glyptapanteles</i>	40	10
<i>Illidops</i>	30	4
<i>Diolcogaster</i>	25	5
<i>Iconella</i>	25	2
<i>Pholetesor</i>	20	5
<i>Protapanteles</i>	20	4
<i>Choeras</i>	15	4
<i>Fornicia</i>	10	?
<i>Deuterixys</i>	5	2
<i>Distatrix</i>	4	3
<i>Hygroplitis</i>	4	1
<i>Rasivalva</i>	4	1
<i>Snellenius</i>	3	1
<i>Napamus</i>	2	1
<i>Nyereria</i>	1	1
<i>Sathon</i>	1	1
<i>Paroplitis</i>	1	1

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HOST RANGES OF *ALEIODES* SPECIES (HYMENOPTERA: BRACONIDAE), AND AN EVOLUTIONARY HYPOTHESIS

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Abstract – The host range of a parasitoid is one of its most crucial characteristics, but it needs both meaningful definition and extremely careful assessment. *Aleiodes* species are koinobiont endoparasitoids of so-called “macrolepidoptera” larvae (or in a few cases other Lepidoptera families with similar larval behaviour such as some Zygaenidae, Yponomeutidae and Pterophoridae). Because they emerge as adults from mummified host larvae, collections of reared specimens with preserved host remains can be built up for which the real host identity is unambiguous. Several distinct host range patterns can be recognised among the best known and most abundant European species. Consideration of these, including experimental evidence, suggests that under some circumstances host ranges tend to expand through the recruitment of frequently encountered new hosts, providing a basis for subsequent speciation. The hypothesis that new species arise as specialists as a consequence of this is hard to test directly, but is supported indirectly.

Key words: Braconidae, *Aleiodes*, host range, speciation

Introduction

The host range of a parasitoid species is one of its central properties, linking its evolutionary past with its present autecology. Through knowledge of the host range of parasitoids we can not only understand and predict their behaviour within current ecosystems, but also gain some understanding of the speciation processes that brought them into existence.

It is not, however, easy to define very sharply what is meant by host range. Fuller arguments are given elsewhere (Shaw 1994) for adopting a conceptual definition, that “the host range of a particular parasitoid species includes only the species of potential hosts that the parasitoid is usually able to attack successfully, following a pattern of searching behaviour enabling it to encounter them regularly”. This rather loose definition is essentially practical: it was designed to address some of the problems that had inhibited the development of useful concepts of host range in the past. The definition has the following main implications:

First, it implies that some perfectly correct rearing records should be discounted if they represent only freak events – of no importance to the autecology of the parasitoid or the host, and lacking in phylogenetic significance. Accepting that such abnormal events, even if genuine, are to be discounted is the only way to ensure that erroneous records will be similarly marginalised (this can only happen, of course, if they are not reinforced regularly by the underlying error of interpretation being repeated). It is the wholly erroneous records (which are unfortunately extremely frequent in the literature, and often repeatedly copied without citation from one publication to another) that will have the most distorting effects on perceptions of host range, so finding a way to marginalise them is vitally important.

Second, it suggests that a quantitative expression of rearing data needs to be used in assessing and describing host range. Meaningful summaries can only be made on this basis (cf. Table 1).

Third, it introduces the idea that some hosts within the host range may be intrinsically more central than others that are encountered less frequently, or attacked less enthusiastically or with a less successful outcome. In addition to differentiating between genuine hosts on the grounds of suitability, there is a need to recognise phenological aspects of host range, especially in temperate climates: many parasitoids are plurivoltine yet use univoltine hosts, each available to only one generation of the parasitoid. Sometimes it happens that the parasitoid is (at least locally) entirely dependent on a single host species at one time of year but able to use a wider range of hosts at another (e.g. *Aleiodes nigricornis* Wesmael (Table 2); also the braconid *Dolichogenidea imperator* (Wilkinson), cf. Shaw & Aeshlimann 1994).

Fourth, it allows a further understanding to be developed: that a parasitoid's "realised host range" (i.e. what actually happens) may not be constant either in space or in time (unless, of course, the parasitoid is strictly monophagous). Clearly, the overlap of a parasitoid's spatial distribution with all of its potential hosts will not usually be exact, and the relative abundance of co-occurring hosts will also vary. Recognition of the realised host range at a locus in space and time is often of more practical significance – for example to population dynamicists, conservation biologists or pest control practitioners – than the potential host range of the parasitoid that may be of more interest to the evolutionary ecologist or systematist. In particular, it is regularly seen that a particular parasitoid population can be *de facto* strictly monophagous simply because only one of the species comprising its potential host range is present. An example is the braconid *Cotesia sibyllarum* (Wilkinson) which, in Britain, has only one species of *Limenitis* to use, while in many parts of Europe it has two.

Materials and Methods

Collecting the data needed to establish and understand the host ranges of parasitoids is difficult and requires great care. Dependence on literature records is completely useless for a great number of reasons that have been reviewed thoroughly by Shaw (1994) and Noyes (1994), and it is clear that more careful, quantitative and verifiable methodologies need to be developed. In a long-term study on the taxonomy and host associations of Western Palearctic species of the genus *Aleiodes* (Braconidae: Rogadinae) I have focused on (a) my own, intensive, rearing activities aimed at sampling as wide a range of potential hosts as possible, done under careful protocols designed to minimise error (Shaw 1997): this survey needs to be as wide as possible and has been greatly supported by numerous people who give me the parasitoids they rear; (b) reared specimens in museum collections available for (my own) determination; and (c) my own experimental manipulations, particularly involving species with British populations (including mating, oviposition and rearing trials) to test the limits of host ranges as well as to resolve aggregates of cryptic species that are not easily separable morphologically.

Aleiodes species are koinobiont endoparasitoids. They attack early instar Lepidoptera larvae, almost entirely "macrolepidoptera" but including some "microlepidoptera" genera such as *Zygaena* and *Ypsolopha* and some Pterophoridae, whose suitably-sized larvae have exposed feeding habits. Only a small minority of *Aleiodes* species attack hosts feeding in semi-concealment (e.g. in seed capsules, leaf-packages, or near the soil surface), most of them using hosts that feed in



more or less fully exposed situations. Nearly all species are solitary, but gregarious development is known in a few species world-wide, one of which is European.

Researching the host ranges of *Aleiodes* species has been considerably helped by the fact that pupation occurs inside the shrunk and darkened, but nevertheless often still distinctive, skin of the host larva – and these “mummies” are often present with the adult parasitoid in museum collections, allowing host determinations to be reassessed (it is surprising how very often hosts had been misidentified, even at family level!). The “mummy” is usually formed when the host is in its penultimate instar or sooner.

The names of Lepidoptera species follow Karsholt & Razowski (1996), and for brevity author’s names are not given here.

Results and Discussion

The breadth of host range varies widely, both in terms of phylogenetic spread and also in the more absolute sense of the number of species seen in the (realised) host ranges of particular *Aleiodes* species, a few of which appear to be literally (i.e. universally) monophagous (e.g. *Aleiodes pallidator* (Thunberg) on *Leucoma salicis*), and some to include large numbers of host species (e.g. *A. alternator*, Table 1).

Table 1 Hosts of *Aleiodes alternator* (Nees)

(Literature records from Shenefelt, 1975. The quantitative data in the right hand column suggest that over 50% of the literature records are erroneous and – as all confirmed hosts feed on low plants – indicate a host range summarised as “low-feeding hairy caterpillars in the families Lasiocampidae, Lymantriidae and Arctiidae”. While the last two families are closely related phylogenetically, Lasiocampidae is not)

Host Family	Number of host species recorded in literature	Reared specimens (species)
TORTRICIDAE	4	–
LASIOCAMPIDAE	1	164(3)
THAUMETOPOEIDAE	2	–
LYMANTRIIDAE	5	52(7)
ARCTIIDAE	4	49(12)
NOCTUIDAE	5	–
	21	265(22)

Overall, two major influences are evident as determinants of host range. One is host phylogeny (i.e. all hosts of a particular parasitoid may be closely related to one another) and the other is host ecology (i.e. the parasitoid may use a wider range of hosts, which are similar to one another in terms of feeding environment, behaviour, or morphology, but not all closely related to one another phylogenetically). For the present purposes I will call these two extreme types of host ranges “continuous” (e.g. Table 3) and “disjunct” (e.g. Tables 1 and 2), respectively. At a higher level it is noteworthy that some species-groups (e.g. the putative subgenera *Chelonorhogas* and *Neorhogas*) are tied to phylogenetically restricted groups of hosts while others (e.g. the putative subgenus

Aleiodes) contain apparently closely related species whose hosts – collectively – span many Lepidoptera families (Table 4). Too few host ranges of s. *Chelonorhogas* species are known for it to be possible to assess whether or not co-cladogenesis may have operated, but for s. *Aleiodes* s.str. it seems clear that the major influence on parasitoid radiation has been host ecology.

Table 2 Hosts of *Aleiodes nigricornis* Wesmael (* Lacks host remains. All hosts are Noctuidae, but *Apamea* is not phylogenetically closely related to *Orthosia*. The single record from *Mythimna* appears to be becoming marginalised and may be erroneous)

Hosts	Reared specimens
Overwinter	
<i>Apamea</i> ? <i>crenata</i>	4
<i>Apamea</i> ? <i>monoglypha</i>	1
<i>Apamea</i> ? <i>epomidion</i>	2
<i>Apamea</i> sp.	8
<i>Mythimna ferrago</i> *	1
Summer	
<i>Orthosia gothica</i>	6
? <i>Orthosia gothica</i>	10

Another overlay that is clear is the importance of the parasitoid's searching environment. Very few *Aleiodes* species use both hosts specialised to low plants (grassland or understory) and those specialised to trees and bushes (canopy) – but with the proviso that in certain habitats (e.g. montane heaths) shrubby low plants will sometimes score as canopy. This applies equally to species having continuous (e.g. Table 3) and disjunct (e.g. Tables 1 and 2) host ranges.

Table 3 Hosts of *Aleiodes pulchripes* Wesmael and *A. rugulosus* (Nees) (All hosts are Acronictinae (Noctuidae). The two parasitoids are in the subgenus *Chelonorhogas*)

Host	<i>pulchripes</i>	<i>rugulosus</i>	Hosts on
<i>Acronicta aceris</i>	1		Trees
<i>Acronicta psi</i>	21		Trees
<i>Acronicta tridens</i>	4		Trees
<i>Acronicta psi/tridens</i>	2		Trees
<i>Acronicta</i> sp.	2		Trees
<i>Acronicta auricoma</i>		1	Low plants
<i>Acronicta euphorbiae</i>		2	Low plants
<i>Acronicta menyanthidis</i>		10	Low plants
<i>Acronicta rumicis</i>		3	Low plants
<i>Acronicta</i> sp.		3	Low plants
<i>Simyra albovenosa</i>		11	Low plants
<i>Oxicesta geographica</i>		1	Low plants

Some *Aleiodes* species are univoltine, while others are plurivoltine. Univoltine species show a strong tendency to have continuous host ranges, and the same is true of some plurivoltine species – especially (but not only) if they use plurivoltine hosts. However, a significant proportion of

plurivoltine species have disjunct host ranges, often using different groups of univoltine hosts at different times of year. It is the species with disjunct host ranges that reveal the most about evolutionary processes, both of host recruitment and of parasitoid speciation.

Table 4 Biological knowledge of W. Palaearctic *Aleiodes* (Several species-groups in the subgenus *Aleiodes* contain species that are morphologically extremely close to one another, and it is in these groups particularly that speciation seems to be most active)

Subgenus	Σ Species	Biology verified (MRS)	Host families
<i>Neorhogas</i>	1	1	Sphingidae
<i>Chelonorhogas</i>	32	12	Noctuidae
<i>Aleiodes</i>	60+	31	14 (including Noctuidae)

The parasitoid’s phenology is of course also connected to its host range. Whether univoltine or plurivoltine, different species of *Aleiodes* pass the winter as a mummy, as a small larva overwintering inside an overwintering host larva, or as an adult (Table 5). The latter behaviour is especially adopted by species attacking the larvae of arboreal Geometridae whose eggs hatch very early in spring.

Table 5 Overwintering by British *Aleiodes* species
(Only species for which understanding is good are included)

	univoltine	plurivoltine
In host larva	5	9
As mummy	10	3
As adult	3+	4+

An interesting example of realised host range varying geographically is seen in Britain in the largely plurivoltine species *Aleiodes coxalis* (Spinola) (erroneously said to be univoltine by Shaw 1994). This occurs, rather sparingly, over most of Britain and Ireland as a parasitoid of Satyridae, seeming to depend on *Coenonympha* species for a mid-summer generation but using probably a range of species including *Maniola jurtina* overwinter. In the south-east of England the hesperiid *Thymelicus lineola* occurs, often at high density, with a larva superficially similar to a satyrid and similarly feeding on Poaceae, which *A. coxalis* parasitises heavily. Through this early summer generation *A. coxalis* achieves a much higher level of abundance where *T. lineola* occurs than elsewhere in Britain. As *T. lineola* spreads northwards and westwards in Britain, the concurrent increase of the populations of *A. coxalis* having this disjunct host range is evident, but no research has been undertaken to see what deleterious effect on the satyrid hosts of *A. coxalis* this may have through the process known as “apparent competition”.

There is good evidence (see discussion on especially *Aleiodes alternator* and the *Aleiodes* species using various *Orthosia* species as hosts in Shaw 1994) that hosts have been recruited to *Aleiodes* host ranges individually – i.e. that each host species in a host range has been a specific challenge to be overcome – and from experimental manipulations it is clear that some *Aleiodes* species show a willingness to oviposit into unsuitable hosts, especially if they are physically or behaviourally similar and/or phylogenetically related to suitable ones but occur only in environments

in which the parasitoid does not normally search (in which case the parasitoid progeny are usually encapsulated and killed by the host's defences). If such a host, behaviourally accepted by the parasitoid, regularly appears in the parasitoid's searching environment it seems that it will eventually be recruited because of the selection pressure on the parasitoid to overcome the host's defences.

Once a parasitoid has expanded its host range, and given changing patterns of host occurrence in its searching environment, conditions that promote speciation may be expected to arise – in particular allowing specialisation, initially behavioural, on one part of the host range by parasitoid individuals that then tend to interbreed and adapt to this smaller host range (or single host) in such a way that gene flow between that population and the parent population will become sufficiently restricted for two species to result. In essence this speciation hypothesis asserts that new species arise as specialists, and it predicts that in closely related pairs of species radically different breadths of host range will sometimes be seen. (Such pairs might perhaps be thought of as either “sister species”, or “parent and daughter species”, depending on respectively whether or not the newly evolved species then out-competes its ancestor in respect of the initially shared part of the host range – i.e. for the “parent” to be seen as a “sister” would depend on its having been altered in some way by the speciation event. The evidence in *Aleiodes* is that competitive exclusion of this kind probably does tend to happen, although there are a few apparent species pairs in which the broader host range (? still) does cover the narrower one. Thus there is also a conceptually identifiable hypothetical process that will tend to reduce the disparity in breadth of host range between “parent” and “daughter” as they move towards being “sisters”).

Aleiodes are rather abnormal koinobionts in being synovigenic and having a long adult life. Nevertheless the conclusion that host ranges tend to expand by piecemeal recruitment of host species, largely through a failure of parasitoids to reject initially unsuitable hosts when they encounter them if they have enough characteristics in common with the parasitoid's actual hosts, may apply to koinobionts (though probably not to idiobionts) more generally (Shaw 1994; Shaw & Horstmann 1997). This is not to say, however, that all *Aleiodes* species (or all koinobiont parasitoids) will necessarily be on the path of expanding their host range it is equally evident that many parasitoids manage to remain as specialists, probably as a result of developing highly effective and exclusive host recognition cues.

Unfortunately the above speciation hypothesis is difficult to test at present. A robust molecular phylogeny of the *Aleiodes* species involved would be extremely helpful, and specimens are being stored in ethanol for that purpose. In the meantime one prediction is that “ancient” species that have not undergone substantial host range expansion (i.e. that have remained taxon specialists, even if using a group of closely related hosts) will have had less opportunity to speciate (i.e. they will appear to be the most morphologically isolated species, not having given rise to any very close “new” relatives). The testable prediction is not that taxon-specialists will be morphologically isolated (because the hypothesis is that new daughter species – i.e. behaviourally but not morphologically distinctive – first arise as taxon-specialists), but rather that very morphologically isolated species will be taxon-specialists. This does appear to be the case – with the single exception that *Aleiodes compressor* (Herrich-Schäffer) has aberrant morphology but regularly uses hosts in at least three and probably four families. However, this species attacks hosts entirely concealed in leaf-packages, buds etc, which it reaches with its blade-like metasoma but never contacts with other parts of itself. In other *Aleiodes* species both antennae and tarsi are employed



at length in the host recognition process, and it seems that an important means to embark behaviourally on a path towards speciation through specialisation has been denied to *A. compressor*, even though it has been forced into the initial condition of host-range expansion by the same difficulty of exercising host discrimination.

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TRISSOLCUS SPECIES OF TURKEY: TAXONOMY AND BIOLOGY

(HYMENOPTERA: SCELIONIDAE)

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Abstract – Sixteen species of *Trissolcus* (Hymenoptera: Scelionidae) were recorded from Turkey: *semistriatus*, *grandis*, *basalis* (= *lodosi* Szabó, 1981) **syn. nov.**, *rufiventris*, *saakovi*, *delucchi*, *festivae*, *pseudoturesis*, *simoni*, *djadetshko*, *antakyaensis*, *vassilievi*, *choaspes*, *scutellaris*, *rungsii*, *flavipes*. Taxonomic notes and key to species; distribution in Turkey and adjacent territories and role in biological control of sunflower's pests are given.

Key words: *Trissolcus* spp., Turkey, taxonomy, biology

Introduction

Species of the genus *Trissolcus* Ashmead, 1893 (= *Microphanurus* Kieffer; *Asolcus* Nakagawa) (Hymenoptera: Scelionidae: Telenominae) are very important for biological pest control because all of them are egg parasitoids of economically important Pentatomidae and Scutelleridae (Heteroptera) bug pests.

Morphologically the genus *Trissolcus* is characterized by sculptured frons, 6-segmented antennal clava and bare eyes. Revisions and identification keys to species were done by several researchers (Kozlov 1965; Safawi 1968; Kozlov & Lě 1978; Johnson 1985 a, b; Masner 1976, 1979, 1980). *Trissolcus* species of Middle East, North Africa, and southern Europe were studied by Safawi (1968), later Kozlov & Lě (1977, 1978) revised the Palaearctic species, while Johnson (1985 a, b) that of Nearctic region. Diagnostic characters and species keys were provided by them.

The role of egg parasitoids in biological control of sunn pests was studied in Romania (Rosca *et al.* 1996), Iran (Rassipour *et al.* 1996), Iraq (Zuwain & Al-Khafaji 1996), Lebanon (Mechelany 1996), Pakistan (Mohyuddin 1996), Syria (Sheikh & Al Rahbi 1996). Voegelé (1996) reviewed the role of parasitoids in biological control of sunflower pests in Near East and stated that the sunn pest problem is especially serious in the Middle East countries, India, the former USSR, Greece, Romania, Bulgaria and Morocco.

Studies on the biology and morphology of *Trissolcus* species, mainly parasitoids of *Eurygaster* spp. and *Aelia* spp. in Turkey were made by Zwölfer (1942), Lodos (1961), Brown (1962), Yüksel (1968), Şimşek & Sezer (1985), Memişoğlu (1990), Akıncı & Soysal (1992), Şimşek *et al.* (1994), Tarla (1997), Doğanlar (1999), Tarla & Doğanlar (1999). Recently, Doğanlar (2001) described a new species, *Trissolcus antakyaensis* Doğanlar, 2001, from Antakya, Turkey.



Materials and Methods

Specimens of different species were obtained from several workers of the Plant Protection Institutes of Ministry of Agriculture and some agriculture faculties of Turkey. Part of specimens was reared from their hosts in the laboratory and part was swept in the field. The keys of Masner (1976 1980), Safavi (1968), and Kozlov & Lě (1978) were used for identification of the species.

Table 1 Distribution of *Trissolcus* species in Turkey

Species	Distribution	Literature
<i>semistriatus</i> (Nees, 1834)	Turkey, except Black See Region and Eastern Anatolia	Zwölfer 1942; Lodos 1961; 1982; Yüksel 1968; Memişoğlu 1990; Şimşek <i>et al.</i> 1994; Doğanlar 1999
<i>grandis</i> (Thomson, 1860)	Turkey, except Eastern Anatolia	Lodos 1961; 1982; Yüksel 1968; Akıncı & Soysal 1992; Şimşek <i>et al.</i> 1994, Doğanlar 1999
<i>basalis</i> (Wollaston, 1858) (= <i>lodosi</i> Szabó, 1981, syn. nov.)	Western, Central, South-Eastern Anatolia	Lodos 1982; Memişoğlu 1990
<i>rufiventris</i> (Mayr, 1908)	Central, Southern and South-Eastern Anatolia	Lodos 1961, 1982; Yüksel 1968; Memişoğlu 1990; Şimşek <i>et al.</i> 1994
<i>saakovi</i> (Mayr, 1903)	Antakya	Doğanlar 1999
<i>delucchi</i> Kozlov, 1968	Antakya	Doğanlar 1999
<i>festivae</i> (Viktorov, 1964)	Antakya	Tarla 1997; Doğanlar 1999
<i>pseudoturesis</i> (Rjachovsky, 1959)	Thrace, Antakya	Tarla 1997, Doğanlar 1999
<i>simoni</i> (Mayr, 1879)	Thrace, Southern & South-Eastern Anatolia	Lodos 1961, 1982; Yüksel 1968; Şimşek <i>et al.</i> 1994
<i>djadetshko</i> (Rjachovsky, 1959)	Hatay	Doğanlar 1999
<i>antakyaensis</i> Doğanlar, 2001	Adana, Antakya	Doğanlar 2001
<i>vassilievi</i> (Mayr, 1903)	Southern and South- Eastern Anatolia	Zwölfer 1942; Lodos 1961; Yüksel 1968; Şimşek & Sezer 1985; Şimşek <i>et</i> <i>al.</i> 1994
<i>choaspes</i> Nixon, 1939	South-Eastern Anatolia	Yüksel 1968; Şimşek & Sezer 1985
<i>scutellaris</i> (Thomson, 1860)	Thrace, South-Eastern Anatolia, Aegean Region	Yüksel 1968; Lodos 1982; Akıncı & Soysal 1992; Şimşek <i>et al.</i> 1994
<i>rungsii</i> (Voegelé, 1965)	Thrace	Akıncı & Soysal 1992
<i>flavipes</i> (Thomson, 1860)	Eastern and South- Eastern Anatolia	Lodos 1982

Results

Sixteen species of *Trissolcus* were recorded from different parts of Turkey (Table 1). Most of species, *semistriatus* (Nees, 1834), *grandis* (Thomson, 1860), *basalis* (Wollaston, 1858), *rufiventris* (Mayr, 1908), *simoni* (Mayr, 1879), *vassilievi* (Mayr, 1903), *scutellaris* (Thomson, 1860), *flavipes* (Thomson, 1860) are widely distributed in Turkey, mainly in Western, Southern and South-Eastern Anatolia. Two species, *pseudoturesis* (Rjachovsky, 1959) is known mainly from Thrace

and Antakya and *choaspes* Nixon, 1939 mainly from South-Eastern Anatolia. Other species, *saakovi* (Mayr, 1903), *delucchi* Kozlov, 1968, *festivae* (Viktorov, 1964), *djadetshko* (Rjachovsky, 1959), *antakyaensis* Doğanlar, 2001 are known from Antakya and adjacent territories, while *rungsii* (Voegelé, 1965) from Thrace. The number of species will increase by further investigations in the regions from Eastern and Northern Anatolia.

Key to the Turkish Species of *Trissolcus*

1. Notauli present 2
- Notauli absent 9
2. Hyperoccipital carina present 3
- Hyperoccipital carina absent 5
3. Vertex with continuous hyperoccipital carina 4
- Vertex with hyperoccipital carina interrupted in middle; mesonotum without longitudinal wrinkles; scutellum smooth; 1.1 – 1.3 mm *delucchii*
4. Frons above antennal sockets with sharp transverse carinae; 1.3 to 1.8 mm *flavipes*
- Frons without carinae, at most frontal depression with some striation; mesonotum with distinct longitudinal wrinkles in posterior half; spiracular furrow carinated on propodeum; scutellum anteriorly transversely carinated; 1.4 – 1.8 mm *saakovi*
5. Scutellum reticulate, distinctly finer than that of mesonotum; postmarginal vein of forewing about 2.0 times as long as stigmal vein; 0.9 – 1.4 mm *simoni*
- Scutellum smooth, not sculptured 6
6. Legs, except coxae, yellow red 7
- Legs entirely black or brown 8
7. Stigmal vein of fore wing straight, 0.5 times as long as postmarginal; antennal clava of female about 3.0 times as long as broad; longitudinal striations of 2nd abdominal tergite reach 0.75 length of tergite *choaspes*
- Stigmal vein of fore wing curved, less than 0.5 times as long as postmarginal vein; antennal clava of female 5.0 times as long as broad; longitudinal striations of 2nd abdominal tergite reach 0.5 length of tergite *vassilievi*
8. Postmarginal vein of fore wing 2.5 times as long as stigmal vein; mesonotum with longitudinal striae posteriorly; 1.0 – 1.3 mm *scutellaris*
- Postmarginal vein of fore wing at most 2.2 times as long as stigmal vein; mesonotum with only few striae; 0.8 – 1.2 mm *festivae*
9. Hyperoccipital carina present; mesonotum with longitudinal striae posteriorly; orbital furrow absent; spiracular furrow developed throughout propodeum; 1.8 – 1.9 mm *antakyaensis*
- Hyperoccipital carina absent 10
10. Postmarginal vein of forewing about 2.0 times as long as stigmal vein 11
- Postmarginal vein of forewing less than 1.8 times as long as stigmal vein 15



11. Posterior half of mesonotum with longitudinal striae 12
 - Posterior half of mesonotum without striae 14
12. All femora reddish yellow; 0.9 – 1.3 mm *pseudoturesis*
 - All femora black or dark brown 13
13. Tibiae black, sometimes foretibiae brownish, with dark brown base and apex; scutellum reticulated laterally; 2.0 – 2.7 mm *grandis*
 - Tibiae reddish-yellow, sometimes hind and middle tibiae dark brown medially; scutellum smooth; 0.9 – 2.0 mm *semistriatus*
14. 2nd abdominal tergite with longitudinal striae reaching 0.6 length of tergite; antennal clava of female 4.5 times as long as maximum width; 0.8 – 1.2 mm *djadetshko*
 - 2nd abdominal tergite with longitudinal striae reaching 0.8 length of tergite; antennal clava of female 4.0 times as long as broad, 1.1 mm *rungsi*
15. Pedicel and scapus yellow; mesonotum uniformly reticulate, without striae; 2nd abdominal tergite with longitudinal striae reaching at most 0,25 length of tergite; 0.8 – 1.2 mm *rufiventris*
 - Pedicel black, scapus yellow; mesonotum with longitudinal striae in posterior half; 2nd abdominal tergite with longitudinal striae reaching 0,7 length of tergite; 1.0 – 1.3 mm *basalis*

Discussion

Many species of *Trissolcus* were reared from eggs of sunn pests, *Eurygaster* spp. and *Aelia* spp., layed on cereals, during biological control procedures in several regions of Turkey (Table 2). The number of recorded host species for particular egg parasitoid are: 13 species for *semistriatus*, 12 for *grandis*, 11 for *basalis*, 9 for *rufiventris*; 2-5 for some other species; one host for each of *delucchi*, *antakyaensis*. Some of the *Trissolcus* species were mass-reared in the laboratory for biological control of sunn pests and the green vegetable bug, *Nezara viridula* L.

Many of them are widespread in many countries of Palaearctic region and have a very important role in control of sunn pests (Table 3). The holotype and paratypes of *T. lodosi* Szabó were studied in the Hungarian Natural History Museum in Budapest. They were found as the same species with *basalis* (**syn. nov.**).

Trissolcus semistriatus and *T. basalis* were recorded from 8 countries, *grandis* – from 9, *rufiventris* and *vassilievi* – from 6, other species – from 3-5 countries. In those countries *semistriatus*, *grandis*, and *rufiventris* were mass-reared and released against *Eurygaster integriceps* and *Aelia* spp. and *basalis* was used for biocontrol of *Nezara viridula* worldwide.

Knowledge on systematics, morphology, biology, host-parasitoid relationships, and geographic distribution of *Trissolcus* species is very important for using in biological control.

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Table 2 *Trissolcus* spp. hosts in Turkey

<i>Trissolcus</i> spp.	<i>Eurygaster integriceps</i> Put.	<i>Eurygaster maura</i> L.	<i>Eurygaster austriaca</i> Schr.	<i>Aelia rostrata</i> Boh.	<i>Aelia acuminata</i> L.	<i>Aelia</i> spp.	<i>Nezara viridula</i> L.	<i>Palomena prasina</i> L.	<i>Graphosoma lineatum</i> L.	<i>Graphosoma semipunctatum</i> F.	<i>Eurydema ornatum</i> L.	<i>Eurydema oleraceum</i> L.	<i>Eurydema ventralis</i> Kol.	<i>Dolycoris baccorum</i> L.	<i>Apodiphus amygdali</i> Germ.	<i>Raphigaster nebulosa</i> Poda	<i>Carpocoris</i> spp.
<i>semistriatus</i>	X	X	X	X	X	X		X	X	X	X		X	X			X
<i>grandis</i>	X	X	X	X	X	X		X			X	X	X	X			X
<i>basalis</i>	X	X	X	X	X	X	X			X	X					X	X
<i>rufiventris</i>	X	X	X	X	X	X			X		X						X
<i>saakovi</i>														X	X		
<i>delucchi</i>															X		
<i>festivae</i>	X										X	X					
<i>pseudoturesis</i>	X		X														
<i>simoni</i>	X	X		X									X	X			X
<i>djadetshko</i>													X	X			X
<i>antakyaensis</i>																X	
<i>vassilievi</i>	X	X		X		X			X								
<i>choaspes</i>					X									X			
<i>scutellaris</i>	X										X	X		X			
<i>rungsii</i>						X											
<i>flavipes</i>	X							X									X

Table 3 Importance of some of *Trissolcus* spp. for sunn pests control in the Near East and adjacent countries

<i>Trissolcus</i> species	Iran	Iraq	Turkey	Syria	Romania Moldavia	Morocco	Ukraine	Afghanistan	Turkmenistan	Uzbekistan	Azerbaijan	Lebanon	Pakistan
<i>semistriatus</i>	X	X	X		X		X		X		X	X	
<i>grandis</i>	X	X	X	X	X		X	X	X		X		X
<i>basalis</i>	X	X	X			X	X		X	X	X		X
<i>rufiventris</i>	X	X	X		X		X		X				X
<i>pseudoturesis</i>			X		X								
<i>simoni</i>			X	X	X						X		
<i>festivae</i>			X		X		X		X		X		
<i>vassilievi</i>		X	X	X	X		X				X		
<i>scutellaris</i>			X		X		X						
<i>djadetshko</i>			X		X		X			X	X		

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HOST-RANGE INCREASE AND PHENOLOGY OF *ENCARSIA MERITORIA* GAHAN IN EUROPE (HYMENOPTERA: APHELINIDAE)

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Abstract – A new parasitoid of *Trialeurodes vaporariorum* (Westwood) and *Aleyrodes lonicerae* Walker (Homoptera: Aleyrodidae), identified as a thelytokous strain of the nearctic species *Encarsia meritoria* Gahan (= *Encarsia hispida* De Santis), was firstly recorded in Europe from Italy and Spain in 1991. Later on the species was reported on other hosts, *Bemisia tabaci* (Gennadius) and *Parabemisia myricae* (Kuwana). Recently, *E. meritoria* has been found as the dominant species in the parasitoid complex of the whitefly *Aleurotrachelus rhamnicola* (Goux) (= *A. espunae* Gomez-Menor) in Campania (Southern Italy), where the aphelinid is also associated with new hosts *Aleurotuba jelinekii* (Frauenfeld) and *Siphoninus phillyreae* (Haliday). The phenology of *E. meritoria* related to *A. rhamnicola* is outlined.

Key words: *Aleurotrachelus rhamnicola*, *Aleurotuba jelinekii*, displacement, *Encarsia hispida*, *Siphoninus phillyreae*, whitefly

Introduction

Encarsia hispida De Santis (Hymenoptera: Aphelinidae) is a yellow species of *Encarsia* originally described from Argentina on female specimens obtained from an unknown whitefly on *Salvia splendens* Ker-Gawl. (De Santis 1948). The author considered the new species allied to *Encarsia meritoria* Gahan (Gahan 1927) but distinguishable having eyes with hairs and longer first and fourth funicular segments. Viggiani (1990), after the examination of the type material, synonymized *E. hispida* with *E. meritoria*. Later, Polaszek *et al.* (1992) considered *E. hispida* a valid species, and distinct from *E. meritoria*, having the second funicular segment (Fig. 2) of the female antennae smaller than the following segment and clearly intermediate in size between first (Fig. 1) and third segment (Fig. 3) (in *E. meritoria* Fig. 2 equal in size to Fig. 3), but Schauff *et al.* (1996) confirmed the synonymy between *E. meritoria* and *E. hispida* proposed by Viggiani (1990). Nevertheless, the taxonomic status of *E. hispida* remains controversial (Evans & Castillo 1988; Giorgini 2001; Babcock *et al.* 2001). At present the complex *meritoria-hispida* is included in the *luteola* group with other species having tarsal formula 5-4-5.

Thelytokous females of Italian *E. meritoria* reared at high temperature or fed with antibiotics (tetracycline) produced males (Giorgini & Viggiani 1996; Giorgini 1998; Giorgini 2001). These males show no morphological differences from those belonging to the biparental population of *E. meritoria*. Furthermore, they are able to court, mate and inseminate non-cured thelytokous females (Giorgini 2001). In *E. meritoria* thelytoky appears associated with parthenogenesis-inducing *Wolbachia* (Hunter 1999; Giorgini 2001).

Encarsia meritoria, uniparental strain or *E. hispida* of the authors, was first recorded in Europe (Spain and Italy) in 1991 as parasitoid of *Trialeurodes vaporariorum* (Westwood) and *Aleyrodes*

lonicerae Walker (Avilla *et al.* 1991; Viggiani & Laudonia 1991). Subsequently the aphelinid was recorded from France in *Bemisia tabaci* (Gennadius) (Onillon & Magnet 1996, 2000), where it was also evaluated as biological control agent (Onillon & Maignet 1996; Maignet & Onillon 1997), and as parasitoid of *Parabemisia myricae* (Kuwana) in Italy (Longo *et al.* 1990; Viggiani 1993, 1996).

Other aspects of *E. meritoria*, morpho-biology (Avilla *et al.* 1991), karyotype (Baldanza *et al.* 1999), total protein profile of adult and larva (Caprio & Viggiani 2001), have been investigated.

In this note preliminary data on the host-range increase and phenology of *E. meritoria* are provided.

Materials and Methods

Whitefly pupae on wild and cultivated plants were sampled in several locations, mainly in Campania (Southern Italy). Single parasitized hosts were isolated in gelatine capsules. The emerged adults were mounted on slides and identified.

In particular, a study on the complex of parasitoids of *A. rhamnicola* Goux on *Rubus ulmifolius* Schott was carried out from 1999. For this purpose samplings were taken regularly at two weeks interval in three locations (Agerola, NA; Lauro, AV, Portici, NA). For each sample/locality (25 leaves), at least 50 young instars of the whitefly were examined and dissected. All the parasitized hosts, containing full larvae or pupae, were collected and isolated in gelatine capsules. Samples of the emerged adults of the parasitoids were mounted on slides and identified.

Results

New hosts. At present the known hosts of *E. meritoria* (thelytokous strain) are the following: *Aleurodicus dispersus* Russell (Hernandez *et al.* 2001), *Aleurodicus dugesii* Cockerell (Babcock & Heraty 2000); *Aleuroglandulus malangae* (Polaszek *et al.* 1992); *Aleurotrachelus socialis* Bondar (Evans & Castillo 1998); *Aleurothrixus porteri* (Polaszek *et al.* 1992); *Aleyrodes lonicerae* Walker (Viggiani and Laudonia, 1991); *Bemisia tabaci* (Gennadius) (Polaszek *et al.* 1992); *Lecanoideus floccissimus* Martin *et al.* (Hernandez *et al.* 2001), *Parabemisia myricae* (Kuwana) (Viggiani 1993, 1996); *Siphoninus phillyreae* (uncertain record in Polaszek *et al.* 1992); *Trialeurodes floridensis* (Quaintance) (Gahan 1927); *Trialeurodes vaporariorum* (Westwood) (Avilla *et al.* 1991).

In the present study adults of *E. meritoria* (all females) emerged from the following hosts: *Aleurotrachelus rhamnicola* Goux, *Aleurotuba jelinekii* (Frauenfeld) and *Siphoninus phillyreae* (Haliday) (Laudonia, *pers. comm.*). To all these hosts *E. meritoria* became associated in recent years, presumably after 1990, as the species was not recovered in previous studies (Laudonia & Viggiani 1984; Viggiani & Iaccarino 1985; Viggiani 1988).

Variations in the complex of parasitoids of *A. rhamnicola*. Until 1985 the parasitoid complex associated to *A. rhamnicola* (= *A. espuiae* Gomez-Menor) in Campania included the aphelinids, *Encarsia longicornis* Mercet, *Encarsia asterobemisiae* Viggiani et Mazzone, and *Encarsia pergandiella* Howard; the first species was the most common (Viggiani & Iaccarino 1985). In Sicily, on the same host, *Cales noacki* Howard (Liotta & Sinacori 1986) and *Encarsia lutea* (Masi) was recorded (Viggiani 1988).



When the present study started in 1999, more or less in the same locations, the situation was different: the dominant species was *Encarsia meritoria* Gahan (uniparental strain) and *E. longicornis* played a minor role as *Cales noacki* Howard, the latter recorded for the first time in Campania, but already known as parasitoid of *A. rhamnicola* in Sicily (Liotta & Sinacori 1986). During the subsequent years the dominance of *E. meritoria* was more marked; *C. noacki* was not found and *E. longicornis* resulted rather rare. In a recent sample of 87 puparia of *A. rhamnicola*, 96.5% were parasitized by *E. meritoria* and 3.5% by *E. longicornis*.

On the contrary, the displacement of *E. meritoria* by *E. protransvena* Viggiani on the introduced whitefly *P. myricae* has been recorded (Viggiani 1996).

Phenology of *E. meritoria* on *A. rhamnicola*

A. rhamnicola is a polyphagous and widely distributed species across the Mediterranean Basin. Its puparia may vary in colours from pale to dark (Martin *et al.* 1996). Most common hosts are *Rhamnus* spp., *Rubus* spp. and *Clematis vitalba* (Martin *et al.* 2000). Very few biological data are known for the whitefly (as *Aleurotrachelus* ? sp. n.) (Viggiani & Iaccarino 1985). According to the present observations on *A. rhamnicola* associated to *Rubus ulmifolius* the following phenology can be outlined. The whitefly overwinters in almost all young stages, even some eggs can be found, but second and third nymphs are the most represented. Puparia appear in March-April and adults emerge mostly during May. They oviposit on the new leaves of the host and the first annual generation takes place, with adult emergence in June-July. The subsequent generations (at least one or two) increase the overlapping of adult emergence that continue until late fall.

Encarsia meritoria overwinters mainly as first larval instar in the nymphs (from the second to the fourth instars) of *A. rhamnicola*, but also some full-larvae and pupae can be found only in the last instar nymph of the host. In fact the development of the parasitoid can be classified as idiobiont, when the oviposition takes place in the fourth nymph instar of the host, and as koinobiont, when it takes place in the youngest instars. In fact, in all cases, the adult parasitoids emerge from the fourth nymph of the host. Egg and larva incapsulation has been observed. The first adults emerge in February-March, a peak has been observed in April-May. Subsequently, until late in fall, the aphelinid reproduce continuously, developing several overlapping generations per year, at least 5-6 against 3-4 of the host.

Host puparia parasitized by *E. meritoria* can be rather easily distinguished by those attacked by *E. longicornis*. In the first case, the pupa exhibits heart-beat movement when observed under light and the puparia skin does not show dorsally darkened areas or stripes.

As found for the native *Encarsia tricolor* Foerster (Viggiani & Laudonia 1985), *E. meritoria* can develop one generation per year in an univoltine host, as *A. jelinekii*, and more on polyvoltine whiteflies, as *A. rhamnicola* and *S. phillyreae*.

The case study of *E. meritoria* shows that the fortuitous introduction of an exotic parasitoid may produce marked variations in time and space in the complex of natural enemies associated with several hosts.

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PARASITIDS OF XYLOPHAGUS AND PHLOEOPHAGOUS INSECTS OF THE HUNGARIAN CONIFEROUS TREE SPECIES

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Abstract – In Hungary, besides the most important broad-leaved tree species (*Quercus* spp., *Robinia*, *Populus*, *Fagus* and *Carpinus*) some 15.1% of the forested land is covered by coniferous tree species. The three most important ones are *Pinus sylvestris* (9.1%), *Pinus nigra* (4.2%) and *Picea abies* (1.5%). All the three genera are either economically or ecologically important. In recent years the mass outbreaks of different bark and wood boring insects have caused enormous economic losses in these stands. In our research, completed in 1998-99, through field investigations and laboratory experiments, we assessed phloeophagous and xylophagous insect species, moreover the parasitoid complex of them. There were 24 research plots: 14 plots for *P. sylvestris*; 4 for *P. nigra*; and 6 for *P. abies*. The use of felled trap trees allowed us to determine the species abundance: on *P. sylvestris* 14 Scolitidae, 2 Curculionidae and 3 Cerambycidae species; on *P. nigra* 9 Scolytidae, 2 Curculionidae and 2 Cerambycidae species; and on *P. abies* 13 Scolytidae, 1 Curculionidae and 3 Cerambycidae species were found. A great number of various parasitoid species have been found. Family Pteromalidae (Chalcidoidea) has been represented by 15 species, and 5 of them has recorded first. Further species of families Eurytomidae, Encyrtidae, Eulophidae, Mymaridae (Chalcidoidea), Platygastriidae (Proctotrupoidea), Braconidae, Ichneumonidae (Ichneumonoidea) and Bethyliidae (Chrysidoidea) have also emerged.

Key words: Bark and wood boring insects, Curculionidae, Cerambycidae, Chalcidoidea, Ichneumonoidea, Pteromalidae, Mymaridae, Scolytidae

Introduction

The forest cover of Hungary is 18.6% (Hungarian Forest Service 2001). Besides the most important broad-leaved tree species (*Quercus* spp., *Robinia*, *Populus*, *Fagus* and *Carpinus*), 15.1% of the forested land is dominated by coniferous tree species. The three most important ones are *Pinus sylvestris* (9.1%), *Pinus nigra* (4.2%) and *Picea abies* (1.5%). All the three genera are either economically or ecologically important. Coniferous forests are often situated where the climate and soil conditions are unfavourable for them (marginal stands), and therefore the frequency of xylophagous insect outbreaks is higher than in other stands. In recent years the mass outbreak of different bark and wood boring insects have caused enormous economic losses in these stands.

An extraordinarily great diversity has been observed among the species, either in composition or frequency of pests present in different areas. In addition to abiotic factors of the environment (e.g. temperature), their natural enemies might play a highlighted limiting role up to how many species of them and in what abundance are present. In Hungary, similar investigations were only carried out in the 50's (Györfi 1941), in which the identification of parasitoids reared from different bark beetle species was completed.



Materials and Methods

In our study, made in 1998-99 on typical Hungarian coniferous stands, through field investigations and laboratory experiments, we assessed the phloeophagous and xylophagous insect species and further the parasitoid complex of them.

The observation has had 24 research plots. The *P. sylvestris* plots (14) in: Bak (BA), Bugac (BU), Fenyőfő (FE), Haláp (HA), Iván (IV), Kemenes (KM), Kerekegyháza (KE), Lábod (LA), Nagybajom (NB), Nagydorg (ND), Őrség (ÖR), Pornóapáti (PO), Salgótarján (NO) and Sopron (SO). The *P. nigra* plots (4) in: Budapest (BP), Bugac (BU), Herend (HE) and Kerekegyháza (KE). The *P. abies* plots (6) in: Bak (BA), Fenyőfő (FE), Kőszeg (KÖ), Őrség (ÖR), Sopron (SO) and Telkibánya (TB). On every research plot 50-60 trees have been marked and the health conditions have been investigated using the international method (II. level: TC1 & TC2). Trap trees were felled in early spring to induce beetle attack. Attacked trees were taken for laboratory studies into light electors. Species composition and abundance were determined for xylophagous and phloeophagous as well as for the parasitoid complex.

Once the different insects hatching in the bark and in the wood respectively had settled, samples were taken from the basal, stem, and the crown sections, and were subsequently placed into light elector. The pests and their parasites trapped when emerging from the sample and stored frozen until identification. The parasitoids identified do not represent only a typical array of species living on some certain xylophagous or phloeophagous insect species, but show the parasitoid complex of all the insect species occurring in bark and wood in the investigation area.

Results and Discussion

Xylophagous and phloeophagous species abundance are shown in Table 1.

Pinus sylvestris

Three Cerambycid species have been found, and the dominant ones are *Rhagium inquisitor* and *Acanthocinus aedilis*. The Curculionid *Pissodes pini* has emerged also frequently. The most various taxon occurred that of the family Scolytidae, with 14 species in it. The primary species, which is able to kill older Scotch pine stands, *Ips sexdentatus* has presented rare (2 spots). Young trees (till the age of 3-5 years) can be killed by *Hylurgus ligniperda*, *Hylastes opacus* and *Hylastes ater*, but their abundance has seemed also low. The secondary species *Tomicus piniperda* and *Hylurgops palliatus* have occurred in common. From them, *T. piniperda* is able to attack healthy trees and we could observe its damages on many research plots.

Pinus nigra

Besides of Cerambycids and Curculionids we have caught Anobiids from young drying branches too. On black pine the secondary and tertiary bark beetles seemed to be dominant, only *Pityogenes bistridentatus* can be considered as a potentially dangerous species.

Picea abies

The lower number of Cerambycids and Curculionids is typical for Norway spruce. The dominant taxon was family Scolytidae, with high number of primary (*Ips typographus*, *Pityogenes chalcographus*), secondary (*Pityophthorus pityographus*, *Dryocoetes autographus*), and tertiary (*Crypturgus cinereus*) species.

Table 1 Relative dominance of xylo- and phloeophagous species on different conifers

SPECIES	<i>Pinus sylvestris</i>		<i>Pinus nigra</i>		<i>Picea abies</i>	
	Rel. value	Dom. value	Rel. value	Dom. value	Rel. value	Dom. value
Anobiidae						
<i>Anobium</i> sp.	-		0.70%	*	-	
Cerambycidae						
<i>Acanthocinus aedilis</i> (Linné, 1758)	5.73%	***	0.35%	*	-	
<i>Callidium violaceum</i> (Linné, 1758)	-		-		0.01%	*
<i>Monochamus galloprovincialis</i>	0.27%	*	-		-	
<i>Rhagium inquisitor</i> (Linné, 1758)	2.39%	**	0.44%	*	0.30%	*
<i>Tetropium castaneum</i> (Linné, 1758)	-		-		0.02%	*
Curculionidae						
<i>Hylobius abietis</i> (Linné, 1758)	0.03%	*	0.52%	*	0.02%	*
<i>Pissodes pini</i> (Linné, 1758)	5.53%	***	0.96%	*	-	
Scolytidae						
<i>Crypturgus cinereus</i> (Herbst, 1793)	9.71%	***	52.49%	*****	36.53%	*****
<i>Dryocoetes autographus</i> (Ratzeburg, 1837)	-		-		3.31%	**
<i>Hylastes ater</i> (Paykull, 1800)	1.85%	**	-		0.01%	*
<i>Hylastes opacus</i> (Erichson, 1836)	0.07%	*	0.26%	*	0.04%	*
<i>Hylurgops palliatus</i> (Gyllenhal, 1813)	18.91%	****	0.26%	*	0.20%	*
<i>Hylurgops glabratus</i> (Zetterstedt, 1828)	-		0.35%	*	-	
<i>Hylurgus ligniperda</i> (Fabricius, 1787)	0.07%	*	1.48%	**	-	
<i>Ips acuminatus</i> (Gyllenhal, 1827)	1.31%	**	-		-	
<i>Ips amitinus</i> (Eichhoff, 1871)	-		-		0.05%	*
<i>Ips sexdentatus</i> (Börner, 1776)	8.60%	***	-		46.97%	*****
<i>Ips typographus</i> (Linné, 1758)	-		-		-	



SPECIES	<i>Pinus sylvestris</i>		<i>Pinus nigra</i>		<i>Picea abies</i>	
	Rel. value	Dom. value	Rel. value	Dom. value	Rel. value	Dom. value
<i>Orthotomicus laricis</i> (Fabricius, 1792)	2.39%	**	5.50%	***	-	
<i>Orthotomicus robustus</i> (Knotek, 1899)	-		7.60%	***	-	
<i>Orthotomicus proximus</i> (Eichhoff, 1867)	2.90%	**	-		-	
<i>Pityogenes chalcographus</i> (Linné, 1761)	1.48%	**	-		6.43%	***
<i>Pityogenes bistridentatus</i> (Eichhoff, 1878)	0.17%	*	29.08%	****	-	
<i>Pityokteines</i> sp.	1.92%	**	-		-	
<i>Pityophthorus pityographus</i> (Ratzeburg, 1837)	1.35%	**	-		5.47%	***
<i>Polygraphus poligraphus</i> (Linné, 1758)	-		-		0.52%	*
<i>Tomicus piniperda</i> (Linné, 1758)	35.30%	*****	0.01%	*	0.01%	*
<i>Xyloterus lineatus</i> (Oliver, 1795)	-		-		0.09%	*
<i>Xyleborus saxesenii</i> (Ratzeburg, 1837)	-		-		0.02%	*

Parasitoids

Former studies on bark beetle parasitoids and natural enemies (Györfi 1941) indicated a various number of insect species living in or from bark beetles.

According to our investigations Braconids and Pteromalids are the dominant parasitoids, but in general a high number of various parasitoid species haven't been determined yet.

As a result, family Pteromalidae (Chalcidoidea) is represented by 15 species (Table 2). Most of them have already recorded from Hungary (Pteromalidae sp., *Catolaccus ater*, *Dinotiscus colon*, *Heydenia pretiosa*, *Metacolus azureus*, *Rhopalicus guttatus*, *Rh. tutela*, *Rhoptrocerus mitus*, *R. xylophagorum* and *Tomicobia seitneri*). The reared parasitoids, at least those of Pteromalidae, are generalists and well known for other xylophagous and phloeophagous insects. It is the first time that the further 5 species have recorded from Hungary (*Metacolus unifasciatus*, *Karpinskiella pityophthori*, *Dinosticus eupterus*, *Rhoptrocerus brevicornis*, *Rhopalicus brevicornis*). The species, have emerged in low number, are species of families Encyrtidae, Eulophidae, Eurytomidae, Mymaridae (Chalcidoidea), Braconidae, Ichneumonidae (Ichneumonoidea), Platygastriidae, Diapriidae (Proctotrupoidea) and Bethyidae (Chrysidoidea), of which host relations are still not clarified.

In most braconid parasitoid cases the exact species have not been identified. Because of their importance in bark and wood boring insect complex we should carry out further braconid research.

Table 2 Relative and dominance values of parasitoids on different conifers

Parasitoid species	<i>Pinus sylvestris</i>		<i>Pinus nigra</i>		<i>Picea abies</i>	
	Rel. value	Dom. value	Rel. value	Dom. value	Rel. value	Dom. value
Ichneumonoidea						
Braconidae						
Braconidae sp.	0.74	*	-		-	
Doryctinae sp.	4.43	**	-		-	
Euphorinae sp.	0.74	*	-		1.21	**
<i>Bracon</i> sp.	18.08	****	25.00	****	47.58	*****
<i>Coleoides</i> sp.	5.17	***	-		13.31	****
<i>Eubazus</i> sp.	42.07	*****	5.00	**	-	
<i>Dendrosoter</i> sp.	-		-		1.61	**
<i>Rhopalophorus clavicornis</i> (Wesm.)	-		-		4.84	**
Ichneumonidae						
Ichneumonidae sp.	0.37	*	-		-	
<i>Trathala</i> sp.	0.74	*	-		-	
<i>Neutrales</i> sp.	-		2.50	**	-	
Chalcidoidea						
Pteromalidae						
Pteromalidae sp.	-		-		0.40	*
<i>Catolaccus ater</i> (Ratzeburg, 1852)	-		-		0.40	*
<i>Dinotiscus colon</i> (Linné, 1758)	0.74	*	-		-	
<i>Dinotiscus eupterus</i> (Walker, 1836)	0.37	*	-		2.42	**
<i>Heydenia pretiosa</i> (Förster, 1856)	1.11	**	7.50	***	0.81	*
<i>Karpinskiella pityophthori</i> (Bouček, 1954)	2.21	**	-		-	
<i>Metacolus azureus</i> (Ratzeburg, 1844)	0.37	*	-		-	
<i>Metacolus unifasciatus</i> (Förster, 1856)	2.95	**	25.00	****	0.40	*
<i>Rhopalicus brevicornis</i> (Thomson, 1878)	6.64	***	-		4.44	**
<i>Rhopalicus guttatus</i> (Ratzeburg, 1844)	3.32	**	-		0.40	*
<i>Rhopalicus tutela</i> (Walker, 1836)	4.06	**	-		5.65	***
<i>Rhoptrocerus mitus</i> (Walker, 1834)	-		-		6.05	***
<i>Rhoptrocerus brevicornis</i> (Thomson, 1878)	-		17.50	****	-	
<i>Rhoptrocerus xylophagorum</i> (Ratzeburg, 1844)	0.37	*	-		2.82	**

Parasitoid species	Pinus sylvestris		Pinus nigra		Picea abies	
	Rel. value	Dom. value	Rel. value	Dom. value	Rel. value	Dom. value
<i>Tomicobia seitneri</i> (Ruschka, 1924)	-		-		2.42	**
Encyrtidae						
Encyrtidae sp.	-		-		0.40	*
Eulophidae						
<i>Aprostocetus</i> sp.	1.11	**	-		-	
Eurytomidae						
<i>Eurytoma</i> spp.	3.69	**	5.00	**	1.61	**
Mymaridae						
<i>Anaphes</i> sp.	-		-		2.02	**
Proctotrupoidea						
Platygastridae						
<i>Platygaster</i> sp.	0.37	*	-		-	
Diapriidae						
Diapriidae sp.	0.37	*	-		-	
Chrysididae						
Bethylidae						
Bethylidae sp.	-		2.50	**	1.21	**

Conclusion

Considering that rearings have not been carried out individually, namely the eclectors have contained several xylophagous species, host-relations cannot be determinated unambiguously. As a result of a long-term project, we supposed to introduce only the list of the already reared xylophagous, phloeoeophagous and parasitoid insects both in species and in their abundance. As the project progresses, the xylophagous – parasitoid species complex reared from newer and newer samples and producing systematically similar results, their statistic probability can be evidences of real host-parasitoid relations. The last main step in this project is the individual rearing of the dominant xylophagous insects.

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THE PARASITOID COMPLEX OF COCCID *SPHAEROLECANIUM PRUNASTRI* FONSCOLOMBE (HOMOPTERA: COCCIDAE) IN THE DANUBE DELTA BIOSPHERE RESERVE IN ROMANIA

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Abstract – Research was done in 10 localities in the Danube Delta Biosphere Reserve during 1992-1994. 1460 specimens of parasitoids obtained from *L*₂ and females of *Sphaerolecanium prunastri*, 378 *L*₂ and 2235 females of *Sph. prunastri* were analysed in total. The host-tree species attacked were *Prunus cerasifera*, *P. cerasifera* var. *pissardii*, *Armeniaca vulgaris*, and *Persica vulgaris*. Six species of primary parasitoids were identified: *Discodes coccophagus*, *Microterys hortulanus*, *Metaphycus silvestrii*, *Coccophagus lycimnia* (females), and *Coccophagus proximus*; and two species of secondary parasitoids: *Cerapterocerus mirabilis* and *C. lycimnia* (males). The total percentage of parasitization in the *L*₂ was 8.5%, which from 7.7% by *C. lycimnia* and 0.8% by *M. silvestrii*. The total percentage of parasitization in females was between 2.9 and 46.7%. The important parasitoid species were *D. coccophagus* and *M. hortulanus*.

Key words: parasitization percentage, primary parasitoid, secondary parasitoid, host plant, sex ratio, Romania

Introduction

Sphaerolecanium prunastri is widespread throughout Europe, except the most northern parts, Turkey, Israel, Iran, China, Japan and North America (Balachowsky & Mesnil 1935; Kawecky 1968; Tereznikova 1981; Kosztarab & Kozar 1988). In Romania, it is spread from the steppe to the mountains (Săvescu 1952, 1982; Minoiu & Lefter 1984).

Materials and Methods

Observations and sample collectings (tree branches with *Sph. prunastri* larvae and females on them) were done in four localities of the Danube Delta (Sfântu Gheorghe – grindul Buhaz –, Maliuc, Sulina, and C.A. Rosetti) and also in other six localities that are adjacent to the Danube Delta (Beștepe, Murighiol, Mahmudia, Enisala, Iancina and Agighiol) during 1992-1994. Diapaused larvae of the second stage (*L*₂) were collected only from Enisala, in early May 1992.

Tree species attacked by *S. prunastri* were: *Prunus cerasifera* L., *P. cerasifera* var. *pissardii* Ckschn., *Armeniaca vulgaris* Lam., and *Persica vulgaris* Mill. Branches with *L*₂ were put into glass jars, covered with thick tissue. The females were put partly in glass test tubes (one female in each tube), and partly in glass jars (a branch with 20-30 females on it). The tubes were covered with cotton wool. We analyzed 378 diapaused *L*₂, and 2235 females of *Sph. prunastri* and 1460 parasitoid specimens.



Results

We reared 32 parasitoid specimens from two species: *Coccophagus lycimnia* Walker (females) and *Metaphycus silvestrii* Sugonjaev from larvae of L₂ instar of *S. prunastri*. From females we reared 1428 parasitoid specimens which from 1385 specimens were primary parasitoids. Six parasitoid species were identified: We identified 6 species of chalcid parasitoids: *Discodes coccophagus* Ratzeburg, *Microterys hortulanus* Erdős, *Metaphycus silvestrii* Sugonjaev, *Cerapterocerius mirabilis* Westwood (Encyrtidae), and *Coccophagus lycimnia* Walker (males), *Coccophagus proximus* Jasnosh (Aphelinidae) (Table 1).

Table 1 Parasitoid species reared from *Sphaerolecanium prunastri* (females) from the Danube Delta Biosphere Reserve (C. m. = *C. mirabilis*; C. p. = *C. proximus*; C. l. = *C. lycimnia*; D. c. = *D. coccophagus*; M. h. = *M. hortulanus*; M. s. = *M. silvestrii*; A.v. = *A. vulgaris*; (P. c.) – *Prunus cerarifera*; (P.c.p.) – *P. cerarifera* var. *pissardii*; P.v. = *P. vulgaris*; (1) – primary parasitoid; (2) – secondary parasitoid)

Locality	Year	Species					
		D. c. ⁽¹⁾	M. h. ⁽¹⁾	M. s. ⁽¹⁾	C. m. ⁽²⁾	C. p. ⁽¹⁾	C. l. ⁽²⁾ ♂♂
Sf. Gheorghe (P.c.)	1994	2					
Maliuc (P.c.p.)	1992	30	34	4		1	4
Maliuc (P.c.p.)	1993	102	64	12	10	1	
Maliuc (P.c.)	1993	18	44	2	6		1
Sulina (P.c.)	1993	7					1
C.A. Rosetti (P.c.)	1993	5					
Murighiol (P.v.)	1994	57	5	3	9		
Mahmudia (P.c.)	1993	11	99	4	15		2
Beştepe (P.c.)	1993	54	187	4	55		2
Agighiol (A.v.)	1993	103	4		14	1	
Enisala (P.c.)	1992	114	97	22	7		2
Iancina (P.c.)	1993	183	4		12		

Among the primary parasitoids reared from females of *S. prunastri*, the majority of specimens belonged to *D. coccophagus* and *M. hortulanus*, and among the secondary parasitoids, *C. mirabilis* is the dominant one (Table 1).

The qualitative structure of the parasitoid complex of *S. prunastri* from Romania is comparable in general to that presented by Loukia Argyriou & Paloukis (1976) in Greece, by Goanță *et al.* (1974) in Moldavia, by Mitic-Muzina (1967) in Yugoslavia, by Kozar & Sugonjaev (1979) in Hungary, and by Podsiadlo (1981) in Poland (Table 2).

In Romania, in the plane and hill conditions, *D. coccophagus* has four generations per year (a spring generation and three summer generations); the sex ratio was 0.3 males to 1 female in samples from Maliuc, collected from *P. cerasifera* in 1993, and 7.7 males to 1 female in samples from Iancina (Table 3).

Microterys hortulanus has one generation per year in Romania. The sex ratio was comprised between 0.2 males to one female in samples collected from Beştepe and 2.7 males to one female in samples from Enisala.

Table 2 The parasitoid complex of the coccid *Sphaerolecanium prunastri* in certain European countries (GR – Greece, HU – Hungary, MD – Moldavia, PL – Poland, RO – Romania, YU – Yugoslavia); (1) – after Argyriou & Paloukis (1976); (2) – Goanță *et al.* (1974); (3) – Mitic-Muzina (1967); (4) – Kozar & Sugonjaev (1979); (5) – Podsiadlo (1981)

Species	GR (1)	RO	MD (2)	YU (3)	HU (4)	PL (5)
<i>Pachyneuron concolor</i>	+	+	+	+	+	+
<i>Eupelmus urozonus</i>				+		
<i>Discodes coccophagus</i>		+	+	+	+	+
<i>Microterys hortulanus</i>	+	+	+	+	+	+
<i>Metaphycus silvestrii</i>		+	+	+	+	+
<i>Cerapterocerus mirabilis</i>		+	+	+	+	+
<i>Blastothrix sericea</i>				+		
<i>Blastothrix erythrostethus</i>		+				
<i>Cheiloneurus claviger</i>		+		+		
<i>Tetrastichus trjapitzini</i>		+				
<i>Coccophagus lycimnia</i>	+	+	+	+	+	+
<i>Coccophagus differens</i>			+			
<i>Coccophagus proximus</i>		+	+			
<i>Coccophagus excelsus</i>		+				
<i>Coccophagus paleolecanii</i>		+				
<i>Marietta picta</i>		+	+	+		
	3	13	9	10	6	6

Cerapterocerus mirabilis is the main parasitoid of *D. coccophagus*. In Romania, *C. mirabilis* has as many generations as its hosts. The sex ratio was comprised between 0.3 males to one female in samples collected from Beștepe and 5.0 males to one female in samples from Iancina (Table 3).

Table 3 The sex-ratio of the main parasitoids of *Sphaerolecanium prunastri*

Locality	Host plant	Year	<i>M. hortulanus</i>		<i>D. coccophagus</i>		<i>C. mirabilis</i>	
			♂♂/♀♀	♂♂/1♀	♂♂/1♀	♂♂/♀♀	♂♂/♀♀	♂♂/1♀
Sf. Gheorghe	<i>P. cerasifera</i>	1994			1/1			
Maliuc	<i>P.c. pissardii</i>	1992	34/0		22/8	2,8		
Maliuc	<i>P.c. pissardii</i>	1993	18/46	0,4	96/6	16	6/4	1,5
Maliuc	<i>P. cerasifera</i>	1993	4/40	0,1	4/14	0,3	2/4	0,5
Sulina	<i>P. cerasifera</i>	1993			5/2	2,5		
C.A. Rosetti	<i>P. cerasifera</i>	1993			3/2	1,5		
Murighiol	<i>P. vulgaris</i>	1994	3/2	1,5	26/31	1,8		
Mahmudia	<i>P. cerasifera</i>	1993	23/76	0,3	7/4	1,8	6/9	0,7
Beștepe	<i>P. cerasifera</i>	1993	28/159	0,2	26/28	0,9	11/44	0,3
Agighiol	<i>A. vulgaris</i>	1993	1/3	0,3	39/64	0,6	8/6	1,3
Enisala	<i>P. cerasifera</i>	1992	71/26	2,7	61/53	1,2	3/4	0,8
Iancina	<i>P. cerasifera</i>	1993	4/0		162/21	7,7	10/2	5

The total percentage of parasitization of the L₂ was 8.5%, which from 7.7% by *C. lycimnia* and the rest by *M. silvestrii*.

The total percentage of parasitization on *S. prunastri* females varied from 2.9% in samples from Sfântu Gheorghe to 46.7% from Mahmudia. The main parasitoid species were *D. coccophagus* and *M. hortulanus*. We noticed a concurrent relationship for host occupation between these two parasitoid species. *Discodes coccophagus* parasitized from 2.9% of the analyzed females at Sfântu Gheorghe to 35.2% at Iancina, while *M. hortulanus* parasitized between 0% and 41.1% (Table 4).

Table 4 The parasitization of *Sphaerolecanium prunastri* females
(D. c. – *D. coccophagus*; M. h. – *M. hortulanus*; M. s. – *M. silvestrii*; C. p. – *C. proximus*)

Locality	Date of host collection sampling	No. of analysed ♀♀	Total	Parasitized females (%)			
				parasitized by:			
				D. c.	M. h.	M. s.	C. p.
Sfântu Gheorghe	28.05.1994	34	2.9	2.9	0	0	0
Maliuc (P.c.p.)	19.05.1992	215	17.7	7.7	9.3	0.5	0.2
Maliuc (P.c.p.)	17.06.1993	160	28.6	17.5	9.4	1.3	0.6
Maliuc (P.c.)	17.06.1993	166	30.7	6.6	23.4	0.6	0
Sulina	19.06.1993	294	4.1	4.1	0	0	0
C.A. Rosetti	16.06.1993	27	7.4	7.4	0	0	0
Murighiol	04.06.1994	132	29.6	25.8	3.0	0.8	0
Mahmudia	14.06.1993	246	46.7	4.9	41.1	0.8	0
Beştepe	13.06.1993	231	37.2	12.1	24.2	0.9	0
Agighiol	12.06.1993	254	33.8	31.9	1.6	0	0.4
Enisala	21.05.1992	334	45.8	23.4	21.6	0.9	0
Iancina	11.06.1993	142	36.6	35.2	1.4	0	0

Our results are generally comparable with those of different authors from certain European countries (Table 5).

Table 5 The parasitization of *Sphaerolecanium prunastri* in certain European countries
((a) – Kozar *et al.* 1982; (b) – Argyriou & Paloukis 1976; (c) – Goanță *et al.* 1974;
(d) – Mitic–Muzina 1967; (e) – Kozar & Viktorin 1978; (f) – Podsiadlo 1981)

Country	Parasitized females (%)		Main parasitoids
	min.	max.	
Turkey ^(a)		30.0	<i>D. coccophagus</i>
Greece ^(b)	Low percentage		<i>C. lycimnia</i>
Rumanian	2.9	91.9	<i>D. coccophagus</i> and <i>M. hortulanus</i>
Moldavia ^(c)	17.3	80.3	<i>D. coccophagus</i> and <i>M. hortulanus</i>
Yugoslavia ^(d)	64.2	98.6	<i>D. coccophagus</i> and <i>M. lunatus</i>
Hungary ^(e)		80.0-90.0	
Poland ^(f)		80.5	<i>D. coccophagus</i>

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ECOLOGY OF THE EULOPHID PARASITOID COMMUNITY LIVING ON HOSTS OF SPONTANEOUS FLORA LINKED TO CITRUS GROVE (HYMENOPTERA: CHALCIDOIDEA: EULOPHIDAE)

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Abstract – From 1997 to 2001 the leaf miner community of spontaneous plants linked to citrus grove has been studied in Sicily (Italy) to find possible relationships between its parasitoid complex and that one of *Phyllocnistis citrella* Stainton (Lepidoptera, Gracillariidae), key species of newly planted citrus groves. Overall, 35 botanical genera of plants have been sampled, which yielded 38 leaf miner species, one Hymenoptera, 20 Lepidoptera and 17 Diptera. All Lepidoptera and the Hymenoptera resulted to be monophagous or oligophagous, while Diptera resulted to be associated on average with 1.6 genera of plants, with only two species strictly monophagous. On the whole, 33 Eulophid species (Hymenoptera, Chalcidoidea) were reared; on average 2.8 parasitoid species resulted associated with each leaf miner. The host-parasitoid associations were 103; 76 of them (73.8% of all the associations) regard 16 Eulophid species also known as antagonists of *P. citrella*. Parasitoids revealed to have a rather generalist behaviour on their hosts, even if the host-parasitoid associations actually occurring represent only 8.2% of all possible associations (1254) between the examined hosts and parasitoids. Spontaneous plants contribute to maintain parasitoid populations of both native and exotic species, confirming their role as a potential source of useful species.

Key words: natural alternative host, host-parasitoid association, parasitoid communities

Introduction

Native plants are known to supply alternative food and refuge to natural enemies of pests of cultivated plants; they contribute to maintain biological diversity in the agroecosystems (McMurtry & Johnson 1965; Powell 1986; Altieri 1991; Ragusa Di Chiara 1991; LaSalle 1993; Massa *et al.* 2001). This function is helpful when biological control depends on many polyphagous antagonists, as in the case of the citrus leaf miner, *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), presently considered a threat to young citrus plantations. In the Mediterranean countries more than a dozen of parasitoid species belonging to the family Eulophidae (Hymenoptera: Chalcidoidea) have been found as antagonists of this pest. They belong to the parasitoid complex of leaf miners community of spontaneous plants, revealing its role as a potential source for the biological control of noxious species (cf. LaSalle 1993). Two years later the arrival of *P. citrella* in Sicily, we started a research on leaf miners communities of native plants linked to citrus groves to find possible relationships between the parasitoid complex of *P. citrella* and that one of native hosts. In the present paper, carried out with data partly published (Caleca *et al.* 1997; Mineo *et al.* 1997a, b; Rizzo & Mineo 1997; Caleca 1998; Caleca & Lo Verde 1998; Caleca *et al.* 1998; Mineo & Sinacori 1998; Rizzo *et al.* 1999; Massa & Rizzo 2000a, b; Massa *et*

al. 2001), we report the results obtained on the structure of Eulophid parasitoid community living on leaf miners of spontaneous plants (herbs, shrubs and trees) linked to citrus groves.

Materials and Methods

On the whole, from 1997 to 2001 35 botanical genera of plants belonging to spontaneous flora linked to citrus groves have been periodically collected. This flora consists of c. 200 species, mainly herbs and shrubs, which live inside or in the neighbouring of citrus groves. Materials were collected mainly in 11 Sicilian citrus orchards in the provinces of Agrigento and Palermo; additional samples were gathered in Sardinia and peninsular Italy. Leaves infested by leaf miners were placed in Petri dishes with wet paper at 25°C, 65% r.h., and L14:D10. All phytophagous species and relative parasitoids that emerged were mounted and identified (for more details cf. Massa & Rizzo 2000b; Massa *et al.* 2001).

Table 1 Hymenoptera and Lepidoptera leaf miners reared from native plants in Sicily (Caleca *et al.* 1997; Mineo *et al.* 1997a, b; Rizzo & Mineo 1997; Caleca 1998; Caleca & Lo Verde 1998; Caleca *et al.* 1998; Mineo & Sinacori 1998; Rizzo *et al.* 1999; Massa & Rizzo 2000a, b; Massa *et al.* 2001; Massa & Rizzo, *unpubl. data*)

Leaf miners (Hymenoptera and Lepidoptera)	Host plants
<i>Messa hortulana</i> Klug (Tenthredinidae)	<i>Populus nigra</i> L. (Salicaceae)
<i>Acalyptis minimella</i> (Rebel) (Nepticulidae)	<i>Pistacia lentiscus</i> L. (Anacardiaceae)
<i>Caloptilia stigmatella</i> (F.)	<i>Populus nigra</i>
<i>Chrysoesthia drurella</i> (Fabr.) (Gelechiidae)	<i>Atriplex rosea</i> L. (Chenopodiaceae)
<i>Chrysoesthia sexguttella</i> (Thunberg) (Gelechiidae)	<i>Chenopodium album</i> L. (Chenopodiaceae)
<i>Cosmopterix pulchrimella</i> Chambers (Cosmopterigidae)	<i>Parietaria</i> (2 spp.) (Urticaceae)
<i>Calybites phasianipennella</i> (Hubner) (Gracillariidae)	<i>Rumex</i> spp. (Polygonaceae)
<i>Dialectica scalarrella</i> (Zeller) (Gracillariidae)	<i>Borago</i> spp. (Boraginaceae)
<i>Leucoptera malifoliella</i> (Costa) (Gracillariidae)	<i>Crataegus monogyna</i> Jacq. (Rosaceae)
<i>Mompha epilobiella</i> (Denis et Schiffermuller) (Mompidae)	<i>Epilobium hirsutum</i> (L.) (Onagraceae)
<i>Phyllocnistis labyrinthella</i> (Bjerk.) (Gracillariidae)	<i>Populus nigra</i>
<i>Phyllocnistis saligna</i> (Zeller) (Gracillariidae)	<i>Salix alba</i> L. (Salicaceae)
<i>Phyllocnistis unipunctella</i> (Stainton) (Gracillariidae)	<i>Populus nigra</i>
<i>Phyllonorycter corylifoliella</i> (Schrank) (Gracillariidae)	<i>Ulmus</i> sp. (Ulmaceae)
<i>Phyllonorycter dubitella</i> (H.-S.) (Gracillariidae)	<i>Salix pedicellata</i> Desf. (Salicaceae)
<i>Phyllonorycter lantanella</i> (Hubner) (Gracillariidae)	<i>Viburnum tinus</i> L. (Loniceraceae)
<i>Phyllonorycter millierella</i> (Staudinger) (Gracillariidae)	<i>Celtis australis</i> L. (Ulmaceae)
<i>Stigmella aurella</i> (Fabr.) (Nepticulidae)	<i>Rubus ulmifolius</i> Schott (Rosaceae)
<i>Stigmella trimaculella</i> (Haworth) (Nepticulidae)	<i>Populus nigra</i>
<i>Stigmella</i> sp. 1 (Nepticulidae)	<i>Ulmus</i> sp.
<i>Stigmella</i> sp. 2 (Nepticulidae)	<i>Salix pedicellata</i>



Table 2 Diptera leaf miners reared from native plants in Sicily

(Caleca *et al.* 1997; Mineo *et al.* 1997a, b; Rizzo & Mineo 1997; Caleca 1998;

Caleca & Lo Verde 1998; Caleca *et al.* 1998; Mineo & Sinacori 1998; Rizzo *et al.* 1999;

Massa & Rizzo 2000a, b; Massa *et al.* 2001; Massa & Rizzo, *unpubl. data*)

* – host species linked to *Mercurialis annua*

Leaf miners (Diptera)	Host plants
<i>Agromyza hiemalis</i> Becker (Agromyzidae)	<i>Urtica</i> (2 spp.) (Urticaceae)
<i>Liriomyza sp.*</i> (Agromyzidae)	<i>Mercurialis annua</i> L. (Euphorbiaceae)
<i>Euleia heraclei</i> (L.) (Tephritidae)	<i>Smyrnum</i> (2 spp.) (Umbelliferae)
<i>Ophiomyia beckeri</i> (Hendel) (Agromyzidae)	<i>Sonchus</i> (3 spp.) (Compositae)
<i>Scaptomyza flava</i> (Fallén) (Drosophilidae)	<i>Medicago</i> spp. (Leguminosae)
<i>Liriomyza congesta</i> (Becker) (Agromyzidae)	<i>Lathyrus pratensis</i> L. (Leguminosae)
<i>Ophiomyia pulicaria</i> (Meigen) (Agromyzidae)	<i>Reichardia picroides</i> (L.) (Compositae)
<i>Liriomyza huidobrensis</i> (Blanchard) (Agromyzidae)	<i>Brassica</i> spp. (Cruciferae), <i>Diplotaxis erucoides</i> (L.) (Cruciferae)
<i>Ophiomyia cunctata</i> (Hendel) (Agromyzidae)	<i>Reichardia picroides</i> , <i>Sonchus</i> spp.
<i>Phytomyza conyzae</i> Hendel (Agromyzidae)	<i>Inula viscosa</i> (L.) (Compositae), <i>Pallenis spinosa</i> (L.) (Compositae)
<i>Japanagromyza salicifolii</i> (Collin) (Agromyzidae)	<i>Salix alba</i> L. (Salicaceae), <i>Populus nigra</i> L. (Salicaceae)
<i>Liriomyza trifolii</i> (Burgess) (Agromyzidae)	<i>Solanum nigrum</i> L. (Solanaceae), <i>Trifolium</i> spp. (Leguminosae), <i>Brassica</i> spp.
<i>Pegomya hyoscyami</i> (Panzer) (Anthomyiidae)	<i>Beta vulgaris</i> L. (Chenopodiaceae), <i>Chenopodium album</i> , <i>Rumex</i> spp.
<i>Scaptomyza pallida</i> (Zetterstedt) (Drosophilidae)	<i>Atriplex rosea</i> , <i>Beta vulgaris</i> , <i>Brassica</i> spp.
<i>Liriomyza bryoniae</i> (Kaltenbach) (Agromyzidae)	<i>Amaranthus</i> spp. (Amaranthaceae), <i>Brassica</i> spp., <i>Conyza bonariensis</i> L. (Compositae), <i>Heliotropium</i> <i>europaeum</i> L. (Boraginaceae), <i>Sonchus</i> spp.
<i>Liriomyza strigata</i> (Meigen) (Agromyzidae)	<i>Picris echioides</i> L. (Compositae), <i>Euphorbia</i> spp. (Euphorbiaceae), <i>Heliotropium europaeum</i> , <i>Malva</i> spp. (Malvaceae), <i>Senecio</i> spp. (Compositae), <i>Sisymbrium irio</i> L. (Cruciferae), <i>Solanum nigrum</i> L. (Solanaceae), <i>Sonchus</i> spp.
<i>Chromatomyia horticola</i> (Goureau) (Agromyzidae)	<i>Echium plantagineum</i> L. (Boraginaceae), <i>Crepis</i> <i>bursifolia</i> L. (Compositae), <i>Brassica</i> spp., <i>Conyza</i> <i>bonariensis</i> , <i>Malva</i> spp., <i>Reichardia picroides</i> , <i>Senecio</i> spp., <i>Sisymbrium irio</i> , <i>Sonchus</i> spp.

To evaluate the global rate of polyphagy of the leaf miners community, hereafter called “average specialisation” (x), we used a modified function from Thomas (1990) and Ødegaard *et al.* (2000): $x = a/(b\ c)$, where c is the total number of botanical taxa obtained, a is the total number

of leaf miners linked to them, and b is the average number of leaf miners associated with each plant genus. We refer specialisation to the botanical genera and not to species, because we found that the maximum level of food preference shown by leaf miners was toward the genus. The function ranges from 0, that is equal to the maximum rate of polyphagy, to 1, that refers to strictly monophagous species. By analogy, the "average specialisation" (x_I) of the parasitoid community, was expressed with: $x_I = a_I/(b_I c_I)$, where c_I was the total number of leaf miners species, a_I was the total number of parasitoids linked to them, and b_I the average number of parasitoids linked to each leaf miner.

Results

Leaf miners

38 leaf miners species have been obtained from 35 genera of plants, listed in Tables 1 and 2; 20 of them were Lepidoptera, 17 Diptera and one Hymenoptera. On the whole, 67 host-plant associations have been recorded, one involving the Hymenoptera leaf-miner, 20 involving Lepidoptera and 46 Diptera (cf. Table 3).

Table 3 Leaf miners community composition: the average specialization (x) for the entire community resulted 0.56 corresponding to a medium level of polyphagy; the same index calculated separately for Lepidoptera and Diptera shows that the first ones are strictly monophagous ($x = 1$), while the second ones are highly polyphagous ($x = 0.37$)

Phytophagous community	Total	Hymenoptera	Lepidoptera	Diptera
N° of leaf miners	38	1	20	17
N° of associated genera	35	1	15	27
Total N° of host-plant associations	67	1	20	46
Average specialization (x)	0.56	–	1	0.37

On average, we found 1.1 leaf miner per plant; Lepidoptera and Hymenoptera resulted associated with only one botanical genus, while Diptera were on average linked to 1.6 genera of plants. The *average specialisation* (x) of the leaf miner community resulted 0.56, corresponding to a medium rate of polyphagy, but the same index showed different values if calculated separately for Lepidoptera and Diptera (Table 3). The former resulted strictly monophagous ($x = 1$), while the latter were highly polyphagous ($x = 0.37$). Polyphagy refers to species distribution on spontaneous plants and can strongly differ from that the noxious species usually show, as in the case of some *Liriomyza* species, like *L. congesta* (Becker), *L. huidobrensis* (Blanchard), and *L. trifolii* (Burgess), found less frequently on spontaneous flora than they do on cultivated plants. *L. bryoniae* (Kaltenbach), *L. strigata* (Meigen), and *Chromatomyia horticola* (Goureau), instead, showed also on spontaneous plants a high level of polyphagy. The only two monophagous Diptera were the Agromyzidae *Agromyza hiemalis* Becker and a species of *Liriomyza* linked to the *Mercurialis annua* L. Other Diptera leaf miners, as *Euleia heraclei* (L.), *Pegomya hyoscyami* (Panzer), and the species belonging to the genera *Ophiomyia*, *Scaptomyza*, and *Phytomyza* confirmed their plant preference restricted to few botanical species (Table 2).



Parasitoids

We reared parasitoids from all the leaf miners species except for *Calybites phasianipennella* (Hubner). Among them, we obtained 33 Eulophid species, listed in Table 4, and recorded 103 host-parasitoid associations, two of which regarded the Hymenoptera, 61 Lepidoptera and 40 Diptera (Table 5). Moreover, 76 of these associations involved 16 parasitoid species already known as antagonists of *P. citrella* (in bold in Table 4).

Table 4 Parasitoid species obtained from hosts of native plants in Sicily

(Caleca *et al.* 1997; Mineo *et al.* 1997a, b; Rizzo & Mineo 1997; Caleca 1998; Caleca & Lo Verde 1998; Caleca *et al.* 1998; Mineo & Sinacori 1998; Rizzo *et al.* 1999; Massa & Rizzo 2000 a, b; Massa *et al.* 2001; Massa & Rizzo, *unpubl. data*)
In bold: (first column) species also known as antagonists of *Phyllocnistis citrella* Stainton; (fourth column) the most recurring host taxa cited in literature
* – parasitoid species known as antagonists of *P. citrella* in mediterranean countries, other than in Sicily, ** – host species linked to *Mercurialis annua*

Parasitoids (Hymenoptera: Eulophidae)	Natural alternative hosts known till now in Sicily		Number of hosts already known (cf. Noyes 1998)
<i>Apotetrastichus postmarginalis</i> (Bouček)	<i>Stigmella aurella</i> ; <i>Stigmella</i> sp.1	2 Lepidoptera	1 Homoptera (?), 1 Lepidoptera
<i>Apotetrastichus sericothorax</i> (Szelenyi)	<i>Stigmella aurella</i>	1 Lepidoptera	2 Lepidoptera
<i>Baryscapus fossarum</i> Graham	<i>Mompha epilobiella</i>	1 Lepidoptera	2 Lepidoptera
<i>Chrysocharis entedonoides</i> (Walker)	<i>Agromyza hiemalis</i> , <i>Chromatomyia horticola</i>	2 Diptera	8 Diptera
<i>Chrysocharis gemma</i> (Walker)*	<i>Cosmopterix pulchrimella</i> , <i>Stigmella aurella</i> , <i>Chromatomyia horticola</i>	2 Lepidoptera, 1 Diptera	4 Diptera, 8 Lepidoptera , 4 Hymenoptera
<i>Chrysocharis nephereus</i> (Walker)	<i>Chrysoesthia sexguttella</i> , <i>Stigmella aurella</i> , <i>Chromatomyia horticola</i>	1 Diptera, 2 Lepidoptera	13 Coleoptera, 7 Diptera, 56 Lepidoptera , 12 Hymenoptera
<i>Chrysocharis orbicularis</i> (Nees)	<i>Chromatomyia horticola</i> , <i>Liriomyza trifolii</i>	2 Diptera	27 Diptera , 2 Lepidoptera
<i>Chrysocharis pentheus</i> (Walker)	<i>Chrysoesthia sexguttella</i> , <i>Cosmopterix pulchrimella</i> , <i>Chromatomyia horticola</i> , <i>Stigmella aurella</i> , <i>Agromyza hiemalis</i>	2 Diptera, 3 Lepidoptera	6 Coleoptera, 34 Diptera, 50 Lepidoptera , 1 Hymenoptera
<i>Chrysocharis prodice</i> (Walker)	<i>Stigmella aurella</i>	1 Lepidoptera	46 Lepidoptera

Parasitoids (Hymenoptera: Eulophidae)	Natural alternative hosts known till now in Sicily		Number of hosts already known (cf. Noyes 1998)
<i>Chrysocharis pubicornis</i> (Zett.)	<i>Chromatomyia horticola</i>	1 Diptera	55 Diptera, 7 Lepidoptera
<i>Cirrospilus diallus</i> Walker	<i>Cosmopterix pulchrimella</i> , <i>Euleia heraclei</i> , <i>Phyllonorycter corylifoliella</i> , <i>Phyllocnistis saligna</i>	1 Diptera, 3 Lepidoptera	6 Coleoptera, 3 Diptera, 39 Lepidoptera , 6 Hymenoptera
<i>Cirrospilus lyncus</i> Walker	<i>Phyllonorycter corylifoliella</i> , <i>Phyllonorycter lantanella</i>	2 Lepidoptera	1 Diptera, 35 Lepidoptera , 4 Hymenoptera
<i>Cirrospilus pictus</i> (Nees)	<i>Chrysoesthia sexguttella</i> , <i>Chrysoesthia drurella</i> , <i>Cosmopterix pulchrimella</i> , <i>Stigmella aurella</i> , <i>Stigmella trimaculella</i> , <i>Agromyza hiemalis</i> , <i>Caloptilia stigmatella</i> , <i>Japanagromyza salicifolii</i> , <i>Messa hortulana</i> , <i>Phyllocnistis labyrinthella</i> , <i>Phyllocnistis unipunctella</i> , <i>Phyllonorycter corylifoliella</i>	2 Diptera, 9 Lepidoptera, 1 Hymenoptera	5 Coleoptera, 1 Diptera, 46 Lepidoptera , 19 Hymenoptera
<i>Cirrospilus variegatus</i> (Masi)*	<i>Liriomyza congesta</i> , <i>Chromatomyia horticola</i> , <i>Euleia heraclei</i> , <i>Acalypttris minimella</i>	3 Diptera, 1 Lepidoptera	1 Diptera, 15 Lepidoptera
<i>Cirrospilus viticola</i> Rondani	<i>Phyllonorycter corylifoliella</i>	1 Lepidoptera	1 Coleoptera, 6 Lepidoptera
<i>Citrostichus phyllocnistoides</i> (Narayanan)	<i>Acalypttris minimella</i>	1 Lepidoptera	<i>Phyllocnistis citrella</i> , <i>Trioza obsoleta</i> Buckton (?)
<i>Diglyphus isaea</i> (Walker)	<i>Agromyza hiemalis</i> , <i>Chromatomyia horticola</i> , <i>Liriomyza trifolii</i> , <i>Liriomyza</i> sp.**	4 Diptera	37 Diptera , 2 Lepidoptera
<i>Diglyphus minoeus</i> (Walker)	<i>Liriomyza strigata</i> , <i>Liriomyza bryoniae</i> , <i>Liriomyza</i> sp.**, <i>Chromatomyia horticola</i>	4 Diptera	16 Diptera , 2 Lepidoptera
<i>Diglyphus poppoea</i> Walker	<i>Chromatomyia horticola</i>	1 Diptera	1 Diptera
<i>Diglyphus crassinervis</i> Erdos	<i>Chromatomyia horticola</i>	1 Diptera	1 Diptera , 1 Lepidoptera
<i>Elachertus inunctus</i> (Nees)	<i>Cosmopterix pulchrimella</i>	1 Lepidoptera	27 Lepidoptera , 1 Hymenoptera
<i>Hyssopus olivaceus</i> (Thomson)	<i>Mompha epilobiella</i>	1 Lepidoptera	4 Lepidoptera
<i>Hemiptarsenus dropion</i> (Walker)	<i>Chrysoesthia sexguttella</i> , <i>Stigmella aurella</i> , <i>Chromatomyia horticola</i>	1 Diptera, 2 Lepidoptera	2 Coleoptera, 7 Diptera , 7 Lepidoptera , 1 Hymenoptera

Parasitoids (Hymenoptera: Eulophidae)	Natural alternative hosts known till now in Sicily	Number of hosts already known (cf. Noyes 1998)
<i>Necremnus artynes</i> (Walker)	<i>Cosmopterix pulchrimella</i> 1 Lepidoptera	–
<i>Neochrysocharis formosa</i> (Westwood)	<i>Chrysoesthia sexguttella</i> , <i>Cosmopterix pulchrimella</i> , <i>Stigmella aurella</i> , <i>Dialectica scariella</i> , <i>Chromatomyia horticola</i> , <i>Scaptomyza pallida</i> , <i>Liriomyza strigata</i> , <i>Liriomyza trifolii</i> , <i>Agromyza hiemalis</i> , <i>Leucoptera malifoliella</i> 5 Diptera, 5 Lepidoptera	3 Homoptera, 1 Coleoptera, 15 Diptera, 30 Lepidoptera , 7 Hymenoptera
<i>Pediobius metallicus</i> (Nees)	<i>Chromatomyia horticola</i> 1 Diptera	29 Diptera , 13 Lepidoptera, 5 Hymenoptera
<i>Pediobius saulius</i> (Walker)	<i>Phyllonorycter lantanaella</i> , <i>Phyllonorycter corylifoliella</i> , <i>Phyllonorycter millierella</i> 3 Lepidoptera	4 Coleoptera, 46 Lepidoptera , 15 Hymenoptera
<i>Pnigalio agraulis</i> (Walker)	<i>Chrysoesthia sexguttella</i> , <i>Stigmella aurella</i> , <i>Phyllonorycter millierella</i> , <i>Phyllonorycter corylifoliella</i> , <i>Messa hortulana</i> , <i>Caloptilia stigmatella</i> 5 Lepidoptera, 1 Hymenoptera	7 Coleoptera, 3 Diptera, 15 Lepidoptera , 9 Hymenoptera
<i>Pnigalio soemius</i> (Walker)	<i>Chrysoesthia drurella</i> , <i>Chrysoesthia sexguttella</i> , <i>Cosmopterix pulchrimella</i> , <i>Stigmella aurella</i> , <i>Phyllonorycter dubitella</i> , <i>Japanagromyza salicifolii</i> 1 Diptera, 5 Lepidoptera	7 Coleoptera, 30 Diptera, 36 Lepidoptera , 6 Hymenoptera
<i>Ratzeburgiola cristata</i> (Ratzeburg)*	<i>Chrysoesthia sexguttella</i> , <i>Cosmopterix pulchrimella</i> , <i>Stigmella aurella</i> , <i>Liriomyza congesta</i> 1 Diptera, 3 Lepidoptera	2 Lepidoptera
<i>Ratzeburgiola incompleta</i> Bouček	<i>Chrysoesthia sexguttella</i> , <i>Cosmopterix pulchrimella</i> , <i>Agromyza hiemalis</i> , <i>Chromatomyia horticola</i> , <i>Liriomyza</i> sp.**, <i>Phyllonorycter corylifoliella</i> 3 Diptera, 3 Lepidoptera	1 Diptera, 2 Lepidoptera
<i>Semielacher petiolatus</i> (Girault)	<i>Cosmopterix pulchrimella</i> , <i>Stigmella aurella</i> , <i>Agromyza hiemalis</i> , <i>Chromatomyia horticola</i> , <i>Liriomyza</i> sp.** 3 Diptera, 2 Lepidoptera	<i>Phyllocnistis citrella</i>
<i>Sympiesis notata</i> (Zetterstedt)	<i>Cosmopterix pulchrimella</i> 1 Lepidoptera	–

On average, 2.8 eulophid parasitoid species resulted to be linked to each leaf miner, while the average specialisation (x_1) of the parasitoid community was 0.32, corresponding to a rather generalist behaviour. The most generalist species resulted *Cirrospilus pictus* (Nees) (12 hosts), *Neochrysocharis parasit* (Westwood) (10 hosts), *Pnigalio agraulis* (Walker) (6 hosts), *Pnigalio soemius* (Walker) (6 hosts), *Ratzeburgiola incompleta* Bouček (6 hosts), *Chrysocharis pentheus* (Walker) (5 hosts), and *Semielacher petiolatus* (Girault) (5 hosts). However, while 3 parasitoid

species resulted on average linked to each Lepidoptera leaf miner, only 2.3 were averagely linked to Diptera. Moreover, a certain number of parasitoid species show to prefer only one order of hosts (12 showed to prefer Lepidoptera, eight preferred Diptera). Consequently, the *average specialisation* (x_1) calculated separately for Lepidoptera and Diptera ` arasitoid complexes (0.4 and 0.5 respectively) results a bit higher than that calculated for the whole host community (Table 5). During our research, the host preference shown by Eulophid species matched enough the most recurring records reported in literature for them (cf. Table 4), except some cases, whose biology is scarcely known. The richest ` arasitoid complex seems to be that of Lepidoptera leaf miners, being constituted by the highest number of parasitoids (25), comprising high numbers both of polyphagous (13) and less generalist species (12).

Table 5 Parasitoid community composition: the average specialisation of the entire community (x_1) resulted 0.32, corresponding to a high level of polyphagy.

However, host-parasitoid associations actually occurring represented only 8.2% of all possible associations between the examined hosts and parasitoids. On the whole, the richest parasitoid complex was that living on Lepidoptera leaf miners

Parasitoid community	Total	From Hymenoptera	From Lepidoptera	From Diptera
N° of parasitoids	33	2	25	20
N° of parasitoid species preferring a host taxon	20	–	12	8
N° of possible host-parasitoid associations	1254	33	627	561
N° of occurring host-parasitoid associations	103	2	61	40
Occurring/possible associations ratio	8.2%	6%	9.7%	7.1%

Discussion

The analysis of Eulophid parasitoid complex living on leaf miners of native flora showed that it is constituted by a rich community, which has a rather generalist behaviour in the host choice. However, among the 33 species found, 20 seem to prefer only one order of hosts, even if some of them are also reported in literature on others (Table 4). Consequently, the *average specialisation* of the parasitoid communities living on Lepidoptera and Diptera resulted higher than that calculated for the whole leaf miners community. It is confirmed by the number of host-parasitoid associations actually occurring (103), that is only 8.2% of all possible associations (1254) between the examined hosts and parasitoids (Table 5).

In a previous study on herbaceous plants linked to citrus groves, we examined leaf miners phenology and parasitisation incidence during the year (Massa & Rizzo 2000b). It emerged that trends of leaf miners and their parasitoids match quite well, except in autumn, when leaf miners populations increase, differently from parasitoids; the maximum of parasitoids activity on hosts of spontaneous plants resulted from March to June (cf. Massa & Rizzo 2000b). In the same study, we compared the values of parasitisation found on the citrus leaf miner (Caleca *et al.* 1998) and on



hosts of spontaneous plants along the year (Fig. 1). Parasitisation on hosts of spontaneous flora was increasing from the winter to the spring and decreasing onwards; conversely, that on *P. citrella* showed its minimum in May and its maximum between August and September. Between the respective values resulted a negative correlation, statistically significant ($r = -0.60$; $P = 0.04$).

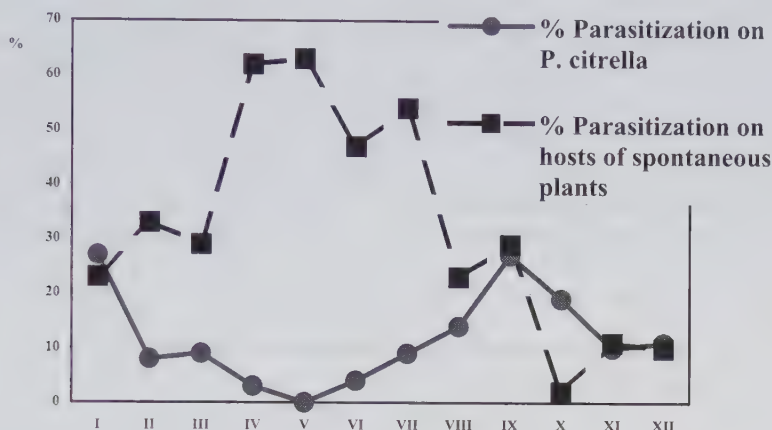


Figure 1 Parasitisation trend on leaf miners of spontaneous plants and on *P. citrella* along the year. Between the two data sets there is a significant negative correlation ($r = -0.60$; $P = 0.04$) (after Massa & Rizzo 2000b)

Spontaneous plants with their variety of hosts let to maintain populations of both native and exotic parasitoid species, as the cases of the two exotic species *Semielacher petiolatus* (Girault) and *Citrostichus phyllocnistoides* (Narayanan) confirm. The first one was known from Australia and Solomon Is. (Bouček 1988; Schauff *et al.* 1998), and considered as a specific antagonist of the citrus leaf miner, being used in several biological control programs in many Mediterranean countries (Michelakis 1997; Argov & Rössler 1996; FAO 1996; Nia *et al.* 1997; Rössler & Argov 1997; Hamed *et al.* 1999). In Sicily it spreads spontaneously in 1998 (Mineo *et al.* 1998), and Massa & Rizzo (2000a) and Massa *et al.* (2001) found it as parasitoid of six new hosts, five of which reported in Table 4 (the sixth host, *Dialectica scalarielli* Zeller on *Echium* sp., was found in Jordan, where the parasitoid spread spontaneously too). The second species, *C. phyllocnistoides*, was previously considered as specific antagonist of the citrus leaf miner (Schauff *et al.* 1998), and it has been actively introduced also in Italy for *P. citrella* biological control (Mineo & Mineo 1999); the record reported here was already cited by Massa *et al.* (2001) on an unidentified Nepticulidae. Even if it seems obvious that alternative hosts helped these species to diffuse and maintain their populations, mainly in the seasons of low availability of *P. citrella* larvae, these facts point out the necessity of improving biological and ecological knowledge of parasitoid species, before using them in biological control programs.

Concluding, researches on the leaf miners community of spontaneous flora and their parasitoids confirm that alternative hosts play the important role of reservoir of natural enemies of phytophagous of cultivated plants. Moreover, Eulophid community living on these hosts, comprising native and exotic antagonists of *P. citrella*, shows a rather generalist behaviour in the

host choice, even if the rate of polyphagy of each parasitoid species is often lower than that the community ecology should let to believe.

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THE PARASITOID COMPLEX OF OAK GALL WASP *ANDRICUS QUERCUSRAMULI* (L.) ♀♂ (HYMENOPTERA: CYNIPIDAE) IN SOUTH EAST ROMANIA

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Abstract – We analyzed 2.195 galls of *Andricus quercusramuli* (L.) ♀♂ from *Quercus pedunculiflora* Koch male flowers from three forests in South-Eastern Romania during 1992-1997. Host-parasitoid relationships for *Ormocerus latus* Walk., *Mesopolobus albitarsus* Walk., *Cecidostiba adana* Askew, *Aulogymnus arsames* Walk., and *Aprostocetus domenichinii* (Erdős) with *A. quercusramuli* are established for the first time as well as for *Aulogymnus testaceoviridis* Erdős. For other 6 species, the parasitoid-host relationships are new for Romania. The host infestation rate by parasitoids obtained from three forests are shown, also flight periods for different parasitoid species are established.

Key words: Cynipidae, *Andricus quercusramuli*, parasitoid complex, Romania

Introduction

Andricus quercusramuli (Linnaeus) (Hymenoptera: Cynipidae: Cynipini) is known as a widespread European species, present all over the country (Brandza 1914; Ionescu 1973). The biology of this species is less studied in Romania, being approached especially from the side of the parasitoid and inquiline studies. Zerova *et al.* (1988) finds it rare, as compared to other species of the *Andricus* genus. The asexual form was not found in Romania until 1959 (Ionescu & Roman 1959). On the other hand, research on gall parasitoids indicates that *A. quercusramuli* is present mainly in the Southern part of Romania (Caruntu 1978; Tudor 1970, 1988; Tudor & Caruntu 1980a, 1980b; Schiopu 1998). Ionescu (1973) and Melika *et al.* (2000) stated that the species develops on six *Quercus* species, but in the surveyed forests we found *A. quercusramuli* galls only on *Q. pedunculiflora*, while three other oak species were presented: *Q. cerris*, *Q. pubescens*, and *Q. virgiliana* (Schiopu 1998).

Fulmek (1968) listed all species of parasitoids and inquilines known at that time from galls of *A. quercusramuli*: 22 chalcids, 1 ichneumonid, and 6 cynipid inquilines. A thorough study on *A. quercusramuli* parasitoid complex was not conducted neither in Europe nor in Romania, and even on a local level. This impelled us to approach the subject.

Materials and Methods

The research was conducted in the extreme SE of Romania, an area of Mediterranean climatic influence (average yearly temperature of 11°C and over 11°C in the immediate vicinity of the Black Sea). The studied forests belong to the *Galio-Quercetum* (*pubescentis*) and *Aceri* (*tatarico*)



– *Quercetum (pedunculiflore)* phytocoenotic associations (Atlas 1979). The Neptun-Comorova nearshore forest with 555 ha is formed mainly of *Q. pedunculiflora*, *Q. pubescens* Willd., and *Q. cerris* L. The Hagieni forest with 393 ha, is partially a natural reserve. It lays 7 km to the SW of the Neptun Comorova forest, and the dominant oak species is *Q. virgiliana* Ten., instead of *Q. cerris*. The Sipote forest is smaller and located 55 km west of the seashore. The dominant species here is *Q. pubescens*. Galls were collected in May and June of 1992, 1994, and 1995 at Hagieni, May, 1995-1997 at Neptun-Comorova and in June, 1987 at the Sipote forest. Collected galls were kept in laboratory conditions for rearing parasitoids. Rate of parasitization, dominance and frequency indexes were calculated, as it shown in Table 2.

Table 1 Data and locations of *Andricus quercusramuli* (L.) ♀♂ parasitoids and inquiline found in Romania

Authors	Locality	Parasitoids and inquilines
Tudor (1970)	Murfatlar (CT)	<i>Eurytoma brunniventris</i> Ratz. <i>Aulogymnus gallarum</i> (L.)
Ionescu (1973)	The Plain of Muntenia	<i>Ceroptres clavicornis</i> Hartig
Caruntu (1978)	Gârboavele (GL)	<i>Synergus variabilis</i> Mayr
Tudor & Caruntu (1980)	Hanu Conachi & Gârboavele (GL)	<i>Aulogymnus arsames</i> Walker <i>Aulogymnus gallarum</i> (L.)
Tudor & Caruntu (1980)	Gârboavele (GL)	<i>Diadegma</i> sp. (Ichneumonidae)
Tudor (1988)	Breazu (IS)	<i>Eurytoma brunniventris</i> Ratz.

Results and Discussion

From 2195 collected galls, 13 chalcid parasitoid species were obtained and identified, along with 2-3 other species which remain unidentified and are marked as Chalcidoidea spp. and Chalcidoidea larvae (Table 2). By the side of actual knowledge (Askew 1961a, 1961b, 1961c, 1961d; Bouček 1966; Bouček & Askew 1968; Erdős 1960, 1961, 1971; Fulmek 1968; Graham 1987; Plugaru 1965), some species are pointed out for the first time as members of this parasitoid complex: *Ormocerus latus* Walk., *Mesopolobus albitarsus* (Walk.), *Cecidostiba adana* Askew, and *Aprostocetus domenichinii* (Erdős). Moreover, for *Aulogymnus testaceoviridis* (Erdős), the host is mentioned for the first time. Species marked with 1, 2, 5, 6, 8, 11, and 13 from Table 2 are new for Romania as members of this complex.

Although Fulmek (1968) mentioned some inquiline species and Ionescu (1973) mentioned *Ceroptres clavicornis*, in our samples we found no inquiline species.

Concerning the presence and role of secondary parasitism in the complex, especially that caused by *Mesopolobus* species and *Eupelmus urozonus*, we have only qualitative data: *M. fasciiventris* was obtained from *A. testaceoviridis* larvae, and an unidentified species was found to parasitize on *A. arsames* larvae. The mortality of gall-inducer larvae varied between 30,45% (8.05.1997) and 43,34% (1.06.1992), with an average of 32,76% for the Hagieni forest. The parasitization rate varied between 27,4% (15.05.1997) and 75,67% (15.05.1995), with an average of 51,51% at the Neptun-Comorova forest. For the entire area and period of research, the parasitization rate had an average of 39,50%.

Table 2 Parasitoid complex of *Andricus quercusramuli* (L.), sexual generation in the forests of SE Romania
(A) = Abundance; (D) = Dominance; (Fr) = Frequency

No.	SAMPLING LOCALITY:	Hagiemi forest – 393 ha; <i>Quercus pedunculiflora</i> Koch, <i>Q. pubescens</i> Willd., <i>Q. virgiliana</i> Ten.				Neptun – Comorova Forest – 555 ha; <i>Quercus pedunculiflora</i> Koch, <i>Q. cerris</i> L., <i>Q. pubescens</i> Willd.				Sipote Forest, <i>Q. pubescens</i>		TOTAL			
		1. 06. 1992	8. 05. 1994	15. 05. 1995	Total	15. 05. 1995	31. 05. 1995	22. 05. 1996	15. 05. 1997	Total	21. 05. 1997	(A) No	(D) %	(Fr) %	(%) rate of infestation
		PARASITOID													
Number of parasitoids / Rate of host infestation															
1. <i>Sycophila biguttata</i> (Swederus)	-	404/27	97/303	13/054	-	-	16/613	-	16/193	-	-	153	17/65	37/50	6/97
2. <i>Torymus auratus</i> Geoffroy	-	282/59	-	282/15	-	-	42/1609	-	24/508	-	-	70	8/07	25/00	3/19
3. <i>Ornocoerus latus</i> Walker	-	20/21	-	20/15	-	-	31/15	-	30/36	-	-	5	0/58	25/00	0/23
4. <i>Mesopolobus albitarsus</i> Walker	-	10/10	-	10/08	-	-	134/76	-	26/314	-	-	27	3/11	37/50	1/23
5. <i>Mesopolobus fasciventris</i> Wstw.	37/31	20/21	-	50/38	-	-	-	-	-	-	-	5	0/58	25/00	0/23
6. <i>Mesopolobus tibialis</i> (Westw.)	-	-	-	-	-	-	-	-	-	-	1/1.47	1	0/12	12/50	0/05
7. <i>Cecidostiba adana</i> Askew	-	-	-	-	-	-	17/623	-	17/206	-	-	17	1/96	12/50	0/77
8. <i>Eupelmus urozonus</i> Dalman	-	-	-	-	-	-	81/2967	-	81/979	-	-	81	9/34	12/50	3/69
9. <i>Aulogymnus arsamus</i> Walker	81/51	-	-	80/62	-	-	-	-	115/02	11/1.33	-	19	2/19	25/00	0/87
10. <i>Aulogymnus gallarum</i> L.	-	70/74	20/62	90/69	68/11	41/46	-	-	101/21	-	-	19	2/19	50/00	0/87
11. <i>Aulogymnus skianurus</i> Ratze.	-	71/074	-	70/54	-	-	-	-	-	-	-	7	0/81	12/50	0/32
12. <i>Aulogymnus testaceoviridis</i> Erd.	-	171/827	185/57	189/454	47/63.51	45/16.48	41/92	-	96/1161	13/19.12	-	298	34/37	75/00	13/58
13. <i>Aprostocetus domenicinii</i> (Erd.)	12/43	272/88	-	282/15	-	41/47	-	-	40/48	-	-	32	3/69	37/50	1/46
Chalcidoidea spp.	717/07	-	51/55	120/92	34/05	62/20	20/77	-	11/1.33	-	-	23	2/65	-	1/05
Chalcidoidea larvae	-	-	-	-	-	-	60/22.99	49/22.37	104-13.18	1/1.47	-	110	12/69	-	5/01
Number of galls collected	41	936	323	1300	74	273	261	219	827	68	-	2195	-	-	-
Number of parasitoids species	3	9	3	10	2	6	5	1	10	2	-	-	-	-	-
Number of obtained parasitoids	19	285	122	426	56	170	140	60	426	15	-	867	-	-	-
Rate of infestation, %	43/34	30/45	37/77	32/76	75/67	62/27	53/64	27/40	51/51	22/16	-	39/50	-	-	-

We found interesting the fact that *A. testaceoviridis*, almost unknown in Western Europe has the highest abundance, dominance, frequency and infestation rate here. It is followed, in decreasing order and at substantial distance, by other primary parasitoids: *Sycophila biguttata*, *T. auratus*, other 3 *Aulogymnus* species and *A. domenichinii*.

Though the two main forests, Hagieni and Neptun-Comorova, are close to each other and the number of parasitoid species was equal, the specific spectrum of parasitoids is not identical, and their ecological efficiency is clearly different. Thus, in the Hagieni forest *M. fasciventris* and *A. skianeuros* were present, however, were absent at the Neptun-Comorova forest. In turn, at Neptun-Comorova *Cecidostiba adana* and *Eupelmus urozonus* were present, which were absent at Hagieni.

Polyphagous species and secondary parasitoids (*M. fasciventris* and Chalcidoidea spp.) had little ecological impact and a minimal influence on the rate of destruction of primary parasitoids in the Hagieni forest. These confirm Askew's statement (1961a) that the predominance of a species within the complex minimizes interspecific destruction same as in the case of *Aulogymnus* species. In the Neptun-Comorova forest, the species that could have been hyperparasitic (*M. albitarsus*, *E. urozonus* and Chalcidoidea spp.) seemed to have played a much more important role, representing 12,93% together (without the Chalcidoidea larvae).

The local performances of secondary parasitoids *M. albitarsus* and *E. urozonus* are worthy of notice; also the inhibition of the main primary parasitoids (*A. testaceoviridis*, *S. biguttata*, and *T. auratus*), and the high performances of Eulophids (*A. testaceoviridis* and *A. gallarum*), in the absence of secondary parasitoids (*Mesopolobus* spp. and *E. urozonus*) and of competitors (*S. biguttata*, *T. auratus*, *A. domenichinii*), in the sample of 15.05.1995. at the Neptun-Comorova forest. The same pattern can be found in the Hagieni forest (especially in the sample of 15.05.1995) where, in the absence of main competitors, *S. biguttata* attains the highest destruction rate: 30,03%.

Also noticeable are geographic differences as compared to England, Germany, Austria (Vienna vicinity), Central Europe, where 4-7 species were part of the complex (Askew 1961a, 1961b; Fulmek 1968). In our area of research we found at least 13 species which from 5 are new in this complex. Species that are almost absent in Western Europe play an important role in the complex here (*A. testaceoviridis*, *M. albitarsus*, *A. domenichinii*). Concerning flight periods, *A. quercus-ramuli* wasps from mid-May till mid-June, with the maximum at the end of May and beginning of June. *Aulogymnus testaceoviridis* wasps in the first two decades of June, with the maximum around 10th of June and a reduced flight in the last decade of next March. *S. biguttata* and *T. auratus* had the same flight period, between May, 20 and June, 10, with the maximum at the end of May. In England, having *Cynips divisa* Htg. as host, these parasitoids had a prolonged flight period, from 10-20 May to 10-15 July, *T. auratus* having a second flight period in September-October (Askew 1961a), *E. urozonus* flies in the second decade of June, and *A. domenichinii* in the first half of June. By the side of *Aulogymnus* species flight period in England (15.04-15.05 or 30.05, Askew 1961d), *A. testaceoviridis* from Romania flies in the first three weeks of June.

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THE PARASITOID AND INQUILINE COMPLEX OF OAK GALL WASP *ANDRICUS VINDOBONENSIS* MUELLNER (HYMENOPTERA: CYNIPIDAE) IN SOUTH EAST ROMANIA

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Abstract – The parasitoid and inquiline complex of *Andricus vindobonensis* in SE Romania is presented. The main parasitoids are *Sycophila variegata*, *Megastigmus dorsalis* and *Ormyrus pomaceus*, while *Eurytoma brunniventris*, *Mesopolobus* sp., *Aulogymnus arsames*, *A. eudoreschus* and *Eupelmus urozonus* are of secondary importance. One inquiline species, *Ceroptres clavicornis* Htg, was found to associate with the gall of *A. vindobonensis*. The specific structure of the complex and the host mortality rate are estimated.

Key words: Cynipidae, parasitoid, inquiline, *Andricus vindobonensis*, Romania

Introduction

Andricus vindobonensis Müllner, 1901 (Hymenoptera: Cynipidae: Cynipini) has a restricted distribution, and known from Austria, Hungary and Romania (Melika 1997; Melika & Bechtold 2001; Ambrus 1974; Buhr 1965; Dalla Torre & Kieffer 1910), more recent data did not reveal its presence in any other parts of Europe (Melika, Csóka & Pujade-Villar 2000; Diakontshuk & Melika 1994; Melika & Csóka 1994; Mikula 1989; Quinlan 1978; Zerova *et al.* 1988). In Romania, the species was found in the southern regions: Bucuresti, Ploiesti, Vlasca, Galati, Constanta (Brandza 1914; Caruntu 1978; Ionescu 1957; Schiopu 1998; Tudor & Tanasescu 1980). Caruntu (1978) mentioned that *A. vindobonensis* may even cause damage in oak forests.

Andricus vindobonensis induces catkin galls on *Quercus cerris* L. only and the only sexual generation is known. The complex of parasitoids and inquilines associated with this gall-inducing cynipid remains largely unknown. Until now, we had only a few literature data on this subject; and no thorough studies on this complex were done (Fulmek 1968; Melika, Csóka). Fulmek (1968) mentioned only *Mesopolobus amaenus* (Walker) reared from galls of *A. vindobonensis*. For Romania only *Cecidostiba fungosa* (Geoffroy in Fourcroy) (= *hilaris* (Walker) and *Mesopolobus fasciiventris* Westwood were reared from this cynipid gall with some quantitative data (Tudor & Tanasescu 1980).

Materials and Methods

The study was conducted in SE Romania, in an area of Mediterranean climatic influence (average yearly temperature of 11°C, and over 11°C in the immediate vicinity of the Black Sea). Two forests located near the meeting point of 45° N parallel and 29° E meridian were choosed.



The Neptun-Comorova forest is located on the Black Sea shore, with an area of 555 ha and formed mainly of three oak species, *Quercus pedunculiflora* Koch, *Q. cerris* L., and *Q. pubescens* Willd. The Canaraua Fetii forest, with natural reserve status, is located right on the 45° N parallel, slightly to the west of the above mentioned intersection point, with an area of 168 ha. Both forests, with *Galio-quercetum (pubescentis)* and *Aceri (tatarico)-quercetum (pedunculiflore)* dominant phytocoenotic associations (Atlas 1979) are 75 km apart, with a few smaller isolated forests in between. In the Neptun-Comorova forest total of 546 galls were collected in June 1994-1996, while in the Canaraua Fetii forest total of 130 galls were collected in June 1995 and 1997. Individual rearing was used. Dissection of galls for studying host-parasitoid relationships was done also. The abundance, dominance, frequency and host infestation ratio were calculated.

Results

From 676 collected galls 183 parasitoids belonging to 8 species, and one inquiline (*Ceroptres clavicornis* Hartig) were reared. All these species, along with the quantitative data related to them, are new for this complex.

Eurytoma brunniventris Ratzeburg (Chalcidoidea: Eurytomidae) and *Eupelmus urozonus* Dalman (Chalcidoidea: Eupelmidae) appeared to be hyperparasitoids of *Sycophila variegata* (Curtis) (Chalcidoidea: Eurytomidae), what is mentioned for the first time in the literature.

The mortality of *A. vindobonensis* caused by parasitoids is between 21.62% (12.06.1995) and 35.38% (13.06.1994), with an average of 29.85%, for the Neptun-Comorova forest and from 14.1 (11.06.1995) to 17.31% (10.06.1997), with an average of 15.38%, in the Canaraua Fetii forest prolong two years. For the entire study period and both forests, the parasitoid-induced mortality was 27.07%.

The inquiline *Ceroptres clavicornis* Hartig (Cynipidae: Synergini) appeared to be a lethal inquiline, causing from 2.75 to 8.91% mortality of gall inducers, with an average 3.85%.

In the Neptun-Comorova forest the total rate of mortality, due to both, parasitoids and inquilines was between 24.86% and 39.6%, with an average 32.6% for the entire period.

At Canaraua Fetii forest the total mortality rate was obviously smaller than in the Neptun-Comorova forest. It was between 23.8% (11.06.1995) and 25.0% (10.06.1997), with an average of 23.84%.

From reared parasitoids, the highest mortality rate of gall inducer was caused by *Sycophila variegata* infestation – 8.88%, *Megastigmus dorsalis* – 5.92%, *Ormyrus pomaceus* – 4.59%, two *Aulogymnus* species, both together – 3.1% and the inquiline, *Ceroptres clavicornis* – 3.85% (see Table 1).

Sycophila variegata and *M. dorsalis* had also the highest frequency levels (see Table 1), while *O. pomaceus* was absent in the samples taken from Canaraua Fetii. This species has only local and temporary importance, like in the samples from Neptun-Comorova forest in 1996, when it caused the highest host mortality rate – 9.18%.

Up to this moment, in Romania, the parasitoids and inquilines known to be associated with *A. vindobonensis* are those listed in Table 1, along with *C. fungosa* and *M. fasciventris*, found by Tudor & Tanasescu (1980) in South Romania, more than 240 km from the area of our study, 10 parasitoids and 1 inquiline species in total are associated with galls of *A. vindobonensis*.

Table 1 The complex of parasitoids and inquilines of *Andricus vindobonensis* from SE Romania
(A) = Abundance; (D) = Dominance; (Fr) = Frequency

SAMPLING LOCALITY:		NEPTUN COMOROVA FOREST, 555 ha				CANARUA FETII							
		<i>Q. pedunculiflora</i> Koch, <i>Q. cerris</i> L., <i>Q. pubescens</i> Willd.				NATURAL RESERVE, 168 ha <i>Q. cerris</i> L., <i>Q. pedunculiflora</i> Koch							
No.	SAMPLING DATE:	13. 06. 1994	15. 06. 1995	12. 06. 1996	TOTAL	11. 06. 1995	10. 06. 1997	TOTAL	TOTAL				
		Number of parasitoids / Rate of host infestation								(A) No	(D) %	(Fr) %	% rate of infestation
PARASITOID													
1.	<i>Megastigmus dorsalis</i> (Fabricius)	21/8,07	7/6,93	7/3,78	35/6,41	3/3,84	2/3,84	5/3,85	40	21,86	100	5,92	
2.	<i>Ormyrus pomaceus</i> (Geoffroy)	9/3,46	5/4,95	17/9,18	31/5,68	—	—	—	31	16,94	60	4,59	
3.	<i>Sycophila variegata</i> Curtis	32/12,30	10/9,90	9/4,86	51/9,34	5/6,41	4/7,69	9/6,92	60	32,79	100	8,88	
4.	<i>Eurytoma brunniventris</i> Ratzeburg	6/2,30	4/3,96	5/2,70	15/2,75	3/3,84	1/1,92	4/3,07	19	10,38	100	2,81	
5.	<i>Mesopolobus</i> sp.	5/1,92	—	—	5/0,91	—	—	—	5	2,73	20	0,74	
6.	<i>Aulogymnus arsamus</i> Walker	4/1,53	—	—	4/0,73	—	—	—	4	2,18	20	0,59	
7.	<i>Aulogymnus eudoreschus</i> Walker	9/3,46	4/3,96	2/1,08	15/2,75	—	2/3,84	2/1,54	17	9,29	80	2,51	
8.	<i>Eupelmus urozonus</i> Dalman	6/2,30	1/0,99	—	7/1,28	—	—	—	7	3,82	40	1,03	
	Number of Galls Collected	260	101	185	546	78	52	130	676				
	Number of Parasitoid Species	8	6	5	8	3	4	4	8				
	Numbers of Parasitoids	92	31	40	163	11	9	20	183				
	Total rate of infestation	35,38	30,69	21,62	29,85	14,10	17,31	15,38	27,07				
Number of inquilines / Rate of infestation of <i>A. vindobonensis</i> galls													
1.	<i>Ceroptries clavicornis</i> Hartig	—	9/8,91	6/3,24	15/2,75	7/8,98	4/7,69	11/8,46	26/3,85	—	80	3,85	

Table 2 Similarity of parasitoid complexes in some *Andricus* species.

(Abbreviations: ce = *Q. cerris*; fr = *Q. frainetto*; pe = *Q. pedunculiflora*; pu = *Q. pubescens*; ro = *Q. robur*,
Aul. ars. = *Aulogymnus arsames*; Aul. eud. = *Aulogymnus eudoreschus*; Cer. clav. = *Ceroptres clavicornis*;
Eup. uroz. = *Eupelmus urozonus*; Eur. brun. = *Eurytoma brunniventris*; Meg. dors. = *Megastigmus dorsalis*;
Orm. pom. = *Ormyrus pomaceus*; Syc. var. = *Sycophila variegata*; Mes. amae. = *Mesopolobus amaenus*;
Mes. fasc. = *Mesopolobus fasciventris*)

No. <i>Andricus</i> spp.	Host species of <i>Quercus</i>	Gene- ration	Meg. dors.	Orm. pom.	Eur. brun.	Syc. var.	Mes. amae.	Mes. fasc.	Eup. uroz.	Aul. ars./eud.	Cer. clav.	Total
1. <i>A. vindobonensis</i>	ce	sex	+	+	+	+	+	+	+	+	+	10
2. <i>A. grossulariae</i>	ce	sex	+	+	+	+	+		+		+	7
3. <i>A. quercusramuli</i>	fr, pe, pu, ce	sex	+		+			+	+	+	+	6
4. <i>A. fecundator</i>	fr, pe, pu, ro	sex	+	+	+	+		+	+			6
5. <i>A. infectarius</i>	ce	sex	+	+	+				+	+		5
6. <i>A. solitarius</i>	fr, pe, pu, ro, vi, ce	asex		+	+				+		+	4
7. <i>A. quercuscalicis</i>	ce	asex			+			+	+			3
8. <i>A. aestivalis</i>	ce	sex	+	+						+		3
9. <i>A. quadrilineatus</i>	pe, pu, ro	both								+		2
10. <i>A. ameni</i>	pe, pu, ro	sex					+		+			2
11. <i>A. seminarius</i>	pe, ro	asex			+							1
TOTAL			6	6	8	3	3	4	8	4	4	

The specific structure of the complex is resembling to that of complexes associated with other *Andricus* species which also induce catkin galls (Askew 1961a, b, 1984; Askew & Neil 1993). As it shown in Table 2, the most similar parasitoid complexes can be find on catkin galls induced by *Andricus grossulariae*, *A. quercusramuli*, *A. fecundator* and *A. infectorius*. Other gall cynipid species, especially asexual generations and those which induce galls on other than *Q. cerris* oak hosts, have very different parasitoid and inquiline complexes.

In the Neptun-Comorova forest where oaks are clearly dominant tree species, we found 8 parasitoid species, with a global host mortality rate of 29.85%, while in the Canaraua Fetii forest, in a rather mixed one, we found only 4 parasitoids, with a parasitization rate of only 15.38%. The main parasitoid species were the same in both forests, *S. variegata* and *M. dorsalis*, but with lower host mortality rates; while *O. pomaceus*, *Mesopolobus* sp., *A. arsames* and *E. urozonus* were not found in the Canaraua Fetii mixed forest. It supports the idea of Garbarczyk *et al.* (1991) that the type of oak forest strongly influence on the specific structure of the parasitoid complex.

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INTERSPECIFIC COMPETITION BETWEEN TWO DIPTEROPHAGOUS PARASITOIDS, *NASONIA VITRIPENNIS* AND *DIBRACHYS CAVUS* (HYMENOPTERA: PTEROMALIDAE), IN BIRD'S NESTS

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Abstract – Field sampling in boxes used by cave-breeding birds proved that the two gregarious ectoparasitoids *Nasonia vitripennis* (Walker) and *Dibrachys cavus* (Walker) (Pteromalidae) occur together in bird's nests. In this special habitat regularly several species of Diptera appear, especially Calliphoridae, whose pupae are of interest for the two parasitoids. In several laboratory experiments, using pupae of *Calliphora vomitoria* as hosts, successive and simultaneous multiparasitism was evoked to examine which species is dominant under different temporal competitive situations. The results show significant limiting influences between the two competitors. In the case of successive multiparasitism, the larvae of *D. cavus* proved to be predators on the larvae and young pupae of *N. vitripennis*. This physical larval attack was responsible for the low mean emerging rates of *N. vitripennis* when *D. cavus* was introduced early. In the reverse case, no significant limiting influence of *N. vitripennis* as the secondary parasitoid on the mean emerging rates of *D. cavus* resulted. When simultaneous competition was tested, *N. vitripennis* dominated significantly over *D. cavus* in the number of successfully parasitized hosts. When both species had to share one fly pupa, their offspring rates were always significantly reduced. Both competitors gain the highest reproductive success when exploiting the host alone. In the case of multiparasitism, *D. cavus* limits the reproductive rate of *N. vitripennis* mainly through interference, while *N. vitripennis* limits the polyphagous competitor indirectly through rapid exploitation of the host resource.

Key words: *Nasonia vitripennis*, *Dibrachys cavus*, Pteromalidae, Calliphoridae, bird's nest, interspecific competition, multiparasitism

Introduction

In bird's nests, we find a rich and at present only poorly investigated community of insects, mites and spiders, which are all classified as nidicole arthropods. As an important part of this very special food-web, several hymenopterous parasitoids control the populations of their hosts, mainly parasites of birds (like the blood-sucking maggots of the blowflies *Protocalliphora*) or consumers of organic waste, faeces or carrion. *Nasonia vitripennis* (Walker 1836) and *Dibrachys cavus* (Walker 1835) are cosmopolitic, gregarious ectoparasitoids of the family Pteromalidae (Chalcidoidea, Hymenoptera). The fact that the two species appear simultaneously in nests of cave-breeding birds is already known since several decades (Woodroffe 1953; Abraham 1985). Extensive studies carried out in the field showed that there is a habitat overlap between both species in nest boxes inhabited mainly by sparrows, starlings and tits, although there are significant differences in the temporal, local and vertical occurrences between the two pteromalids (Abraham 1985; Schlein 1998).



Nasonia vitripennis parasitizes pupae of various cyclorrhaphous flies and is strictly limited in its host range to the order Diptera (like Calliphoridae, Muscidae, Sarcophagidae; Peck 1963). In bird's nests, *N. vitripennis* is the dominant natural pupal parasitoid of the bird-parasitic genus *Protocalliphora* (Peus 1960; Abraham 1985). *Dibrachys cavus* is commonly known as a quite polyphagous species. Its host range includes about 150 species out of 40 families of different orders like Coleoptera, Lepidoptera, Hymenoptera and Diptera (Peck 1963). Although *D. cavus* is regularly recorded from bird's nests, it is unlike *N. vitripennis* not mentioned yet as a parasitoid of the genus *Protocalliphora*.

But as comparable hosts like the carrion-infesting genera *Calliphora* and *Sarcophaga* as well as a lot of Muscidae are often found in bird's nests, competition between the two parasitoids for fly pupae of several species that occur in bird's nests appeared likely. *Dibrachys cavus* is also a notorious hyperparasitoid of other parasitic Hymenoptera, like braconids, ichneumonids and other chalcids, even pteromalids (Peck 1963; Day 1969). So it seemed possible that it developed a facultative hyperparasitic relationship to the strictly dipterophagous competitor *N. vitripennis*.

Materials and Methods

Characteristics of the parasitoids. Both species were obtained through field sampling in nest boxes from June to October, using pupae of *Calliphora vomitoria* as hosts. The rearings and experiments took place in plastic petridishes, stored in the laboratory at 25°C. All used females were fed with cutted raisins and given opportunity for copulation. Specific datas were raised within the laboratory rearings where no interspecific disturbance took place.

Successive interspecific competition. Either 5 females of *N. vitripennis* or 5 females of *D. cavus* were introduced for 48 hours to petridishes, each containing 5 healthy host pupae of *Calliphora vomitoria*. After this incubation time, the primary parasitoid was removed completely and the second species was introduced successively to the already parasitized fly pupae. The intervals between the two introductions varied from the moment directly after removal of the first species to 9 days after the first removal, each interval 24 hours after the previous (10 altogether). Control treatments remained unaffected by a secondly introduced species. Each fly pupa was put in a gelatine capsule to save the possibility of an exact offspring counting. Later, dissections of all puparia were made to count dead stages of the parasitoids. After analysis, further multiparasitized puparia with still developing stages were dissected to find explanations for the experimental results.

Simultaneous interspecific competition. A single host pupa of *Calliphora vomitoria* per petridish was exposed to both species simultaneously in a ratio of 1:1 females for 24, 48 or 72 hours. The fly pupae were then removed and stored isolated in gelatine capsules until wasps emerged. The offspring was recorded and all fly puparia were dissected.

Statistical analysis. Frequencies were calculated with the χ^2 -test, mean values with the Mann-Whitney-U-test, Kruskal-Wallis-test or Wilcoxon-test.

Results

The main period of simultaneous activity in (often the same) nest boxes proved to be June, July and August. The offspring of *N. vitripennis* mostly remains in larval diapause starting significantly

in July, whereas *D. cavus* produces offspring without any diapause until autumn. The following characteristics were obtained in the laboratory at 25°C.

Table 1 Specific characteristics. Mean time of development (egg-adult) in days, sex ratio (male:female), mean rate of emerging adults per fly pupa parasitized by 1 female for 24 hours, and maximum of counted emerging adults per fly pupa after various superparasitism

	Mean time	Mean sex ratio	Mean rate/pupa	Max. Rate
<i>N. vitripennis</i>	14,7 d (n = 112)	1:5 (n = 130)	33,1 (n = 25)	92
<i>D. cavus</i>	21,9 d (n = 148)	1:7 (n = 130)	13,1 (n = 23)	58
Mean difference	7,3 d (p<0,001)	– (p<0,01)	20,0 (p<0,001)	–

Outcome of successive competition

Nasonia vitripennis primary, *Dibrachys cavus* successive parasitoid.

145 pupae were considered. From 138 fly pupae adult wasps emerged (of 7 only dead pupae of *N. vitripennis* were recorded). Out of 81 (58,7%) fly puparia *N. vitripennis* emerged, out of 18 (13,0%) *D. cavus* and out of 39 (28,3%) adults of both species resulted. On 108 hosts (74,5%) dead pupae of *N. vitripennis* occurred; from 42 (38,9%) of these 108 fly pupae *D. cavus* adults emerged. On only 8 (5,5%) hosts dead pupae of *D. cavus* were found.

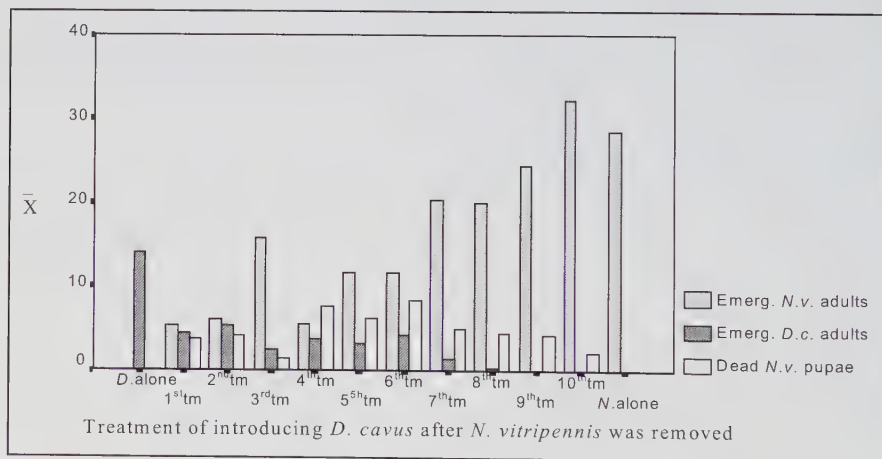


Figure 1 Mean rates of emerging adults / host individual after successive introduction of *D. cavus* to previously *N. vitripennis*-parasitized (48 h) host pupae with varying intervals (1st-10th treatment)

The influence of the time interval on the mean number of emerging wasps per host pupa proved to be very significant for both species ($p < 0,01$). The influence of the time interval on the mean number of dead *N. vitripennis* pupae was significant ($p < 0,05$), but not on the mean number of dead *D. cavus* pupae. The mean values of control treatments were significantly higher in most cases (*N. vitripennis*: 1st-6th treatments, $p < 0,01$; *D. cavus* : all; 1st-8th treatments $p < 0,05$).

Dibrachys cavus primary, *Nasonia vitripennis* successive parasitoid.

A total number of 91 pupae was considered. From 82 fly pupae adult wasps emerged (in 9 puparia only dead pupae of *D. cavus* were found). From 64 pupae (78,0%) *D. cavus* resulted, just from 7 (8,5%) *N. vitripennis*. Adults of both species were recorded from 11 (13,4%) hosts. On 29 hosts (31,9%) dead pupae of *D. cavus* occurred, on only 3 (3,3%) dead pupae of *N. vitripennis*. From the 29 puparia including dead pupae of *D. cavus*, only 3 (10,3%) gave emergence to *N. vitripennis*.

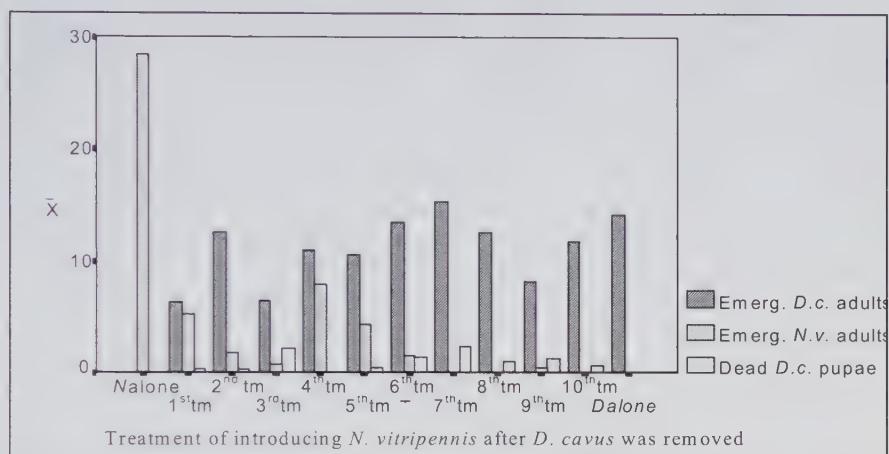


Figure 2 Mean rates of emerging adults / host individual after successive introduction of *N. vitripennis* to previously *D. cavus*-parasitized (48 h) host pupae with varying intervals (1st-10th treatment)

The influence of the time interval on the mean number of emerging *D. cavus* adults per host pupa proved to be not significant, as well as on the mean number of its dead pupae. The influence of the time interval on the mean number of emerging *N. vitripennis* adults became significant ($p < 0,05$). The mean value of the control treatment was always significantly higher for *N. vitripennis* ($p < 0,01$), but almost never for *D. cavus* (except 1st tm, $p < 0,05$).

Results of dissections by direct observation

Multiparasitized hosts of the treatments with the highest pupal mortality of *N. vitripennis* as the primary parasitoid (4th, 5th and 6th treatments) were dissected. Larvae of *D. cavus* were regularly observed when feeding on old (passive) larvae and young or middle-aged pupae of *N. vitripennis*. This only appeared to happen when the fly pupae were already nearly or fully mummified and exhausted as a food resource.

Outcome of simultaneous interspecific competition

None of the exposed fly pupae survived. Differences in mean emerging rates between the three experimental durations (24, 48 or 72 hours) were not significant and are therefore not figured here. Out of 137 exposed fly pupae altogether, adults of only *N. vitripennis* emerged from 71 pupae

(51,8%), of only *D. cavus* from 46 pupae (33,6%) and of both competitors from 20 pupae (14,6%). These differences are highly significant ($p < 0,001$).

Table 2 Simultaneous interspecific competition. Mean emerging rates per host pupa

	1 species emerged	both species emerged	reduction to (%)
<i>N. vitripennis</i> (71 : 20 cases)	20,6	5,4	26,2%
<i>N. v.</i> males	5,0	2,0	40,0%
<i>N. v.</i> females	15,6	3,4	21,8%
<i>D. cavus</i> (46 : 20 cases)	12,0	4,2	35,0%
<i>D. c.</i> males	2,1	1,2	57,1%
<i>D. c.</i> females	9,9	3,0	30,3%

The mean emerging rates per host pupa decrease significantly ($p < 0,001$) when the species have to share one host pupa with the competitor (Tab. 2). This also proved to be significant compared with control batches containing fly pupae that were not exposed to both species but only to one.

Discussion

When two (or more) parasitoid species compete for similar host species in the same habitat, several intrinsic (larvae on the same host individual compete by means of physical attack or physiological suppression in case of multiparasitism) and extrinsic (females compete for oviposition sites) factors exist (Salt 1961; Wylie 1972; Steinberg *et al.* 1987; Alebeek *et al.* 1993). The results shown in this paper mainly deal with the intrinsic level of larval competition on one host by means of physical combat or suppression through starvation. There are plenty of cases in parasitoid literature. In similar experimental designs like in the present work, successive and simultaneous interspecific competition and multiparasitism were evoked for example by Wylie (1972); Van-Strien-Van Liempt (1983); Pawson *et al.* (1987); Bai & Mackauer (1991); Alebeek *et al.* (1993); Leveque *et al.* (1993); or Gauthier *et al.* (1999). Of course, also extrinsic factors like searching ability, egg laying capacity, aggressive behaviour between the ovipositing females, interspecific host discrimination and ovicide had surely influence on the outcome of the experiments.

Successive interspecific competition. *N. vitripennis* is significantly disturbed in its development when females of *D. cavus* multiparasitize the host pupae. The degree of this limiting effect of the polyphagous species on *N. vitripennis* depends significantly on the moment of multiparasitization. The earlier introduced females of *D. cavus* were able to parasitize hosts that were firstly accepted by *N. vitripennis*, the higher was their mortal effect on the *N. vitripennis* larvae or younger pupae (see Fig. 1). In the reverse situation, multiparasitization by females of *N. vitripennis* did not have a comparable and significant negative influence on the development of *D. cavus*. The mean number of emerging wasps per host individual did not change significantly for *D. cavus* in dependence on the time of introducing *N. vitripennis* females (see Fig. 2). None of the two pteromalid species could reach as high emergence rates when being the secondary parasitoid as when using the *Calliphora* pupae alone (see control treatments in Figs 1-2). The reasons for these results could be revealed by dissections. The polyphagous larvae of *D. cavus* are predators on the larvae and young pupae of *N. vitripennis* and are responsible for the mortality of the competitors early



developmental stages. Larvae of *D. cavus* were regularly observed when sucking out young or middle aged pupae of *N. vitripennis*, but only when the primary host, the fly pupa, was nearly or fully exploited as a food resource. *N. vitripennis* larvae showed no aggressive, predatory tendencies against the competitor. Its larval diet exclusively depends on the fly pupa resource.

Dibrachys cavus, known as a very polyphagous species, accepts young stages of *N. vitripennis* as a food substitute for the already exhausted and mummified primary host. *D. cavus* could be defined as a facultative predator in short supply of larval food. Which species is dominant according to the number of emerging wasps strongly depends on the present developmental stages and the temporal relationship when the "conflict" situation of host sharing starts. It became obvious that *D. cavus* cannot be defined as a hyperparasitoid of *N. vitripennis* in bird's nests. Its lethal influence on *N. vitripennis* larvae and young pupae in the case of multiparasitism is a facultative predatory strategy of evasion when in poverty of the preferred food resource, the fly host. This seems to be correct as the reproductive rate of *D. cavus* is always suboptimal when sharing the host with *N. vitripennis*.

Wylie (1972) evoked larval competition in comparable experiments between *N. vitripennis* and either *Muscidifurax raptor* or *Spalangia cameroni* by successive or simultaneous parasitization of *Musca domestica* pupae. There, *N. vitripennis* also often succeeded due to a rapid host utilization and fast development, leaving the competitors to starve, but showed no larval aggression. On the other hand, the larvae of the rival species were predaceous on young stages of *N. vitripennis* and therefore behaved similar to the larvae of *D. cavus* in the present work. Propp & Morgan (1983) investigated the multiparasitism of *Spalangia endius* and *Muscidifurax raptor* on pupae of *Musca domestica* with similar methods. They point out that oviposition restraint and the ability of host discrimination influenced the decrease of multiparasitism as the time after the initial parasitization increased, also caused by inner cues and markers. Of course, mechanisms like this might have been effective also in the successive competition between *N. vitripennis* and *D. cavus* in the present case, surely in the later treatments. *N. vitripennis* is known for its highly developed inter- and intraspecific discrimination capacities (Wylie 1965; Wylie 1970; Rivers 1996). So, possibly, in later treatments the acceptance of the previously *Dibrachys*-parasitized host pupae was already low for *N. vitripennis* and therefore multiparasitism did not occur as continual as in the reverse case.

Simultaneous interspecific competition. Within a short period of time (24 until 72 hours), much more hosts were successfully parasitized by *N. vitripennis* than by *D. cavus* females. This result indicates the close host adaptation of the strictly dipterophagous species. The polyphagous *D. cavus* gained relative low rates of parasitization. The domination of *N. vitripennis* is likely caused by more effective and specialized behavioural and physiological mechanisms and sensual efficiency. When competition is evoked simultaneous, extrinsic advantages work in favour of *N. vitripennis*. If wasps of both species emerged out of one host pupa, their mean number was always significantly lower when compared to hosts from which adults of only one species resulted (see Table 2). *N. vitripennis* was more affected by this mean reduction than *D. cavus*, due to the latter's predatory larvae; females of both species were more affected than males (see Table 2).

Conclusion

In the case of multiparasitism, *D. cavus* limits the reproductive rate of *N. vitripennis* mainly through interference (directly), while *N. vitripennis* limits the polyphagous competitor through

rapid exploitation of the host resource (indirectly), caused by a faster development and higher offspring rate per fly pupa. In the experiments, the confrontation of the ovipositing females was strongly and unnaturally evoked in petridishes on a very limited space with a high pressure of host sharing and an impossibility of evasive behaviour.

In the field, of course, effective evasion strategies and therefore competition limitation are possible. Inside the nest habitat, extrinsic advantages are likely much more important for the reproductive success of the pteromalids than intrinsic advantages when multiparasitization occurs. To give a realistic assessment of the actual competitive intensity in the field, further research made by the author concentrates on differences on the extrinsic level, especially by means of foraging behaviour, host detection and discrimination abilities, olfactory sensibility and preferences as well as habitat use and dispersal. The specific differences on the extrinsic level lead to niche differentiation inside the bird's nest habitat and a counter-balanced coexistence of *N. vitripennis* and *D. cavus* under natural conditions. These findings are currently prepared for publication.

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ACTIVITY OF *SCHIZONOTUS SIEBOLDI* RATZEBURG (HYMENOPTERA: PTEROMALIDAE) ON POPLAR LEAF BEETLE PUPA, ON SEVEN DIFFERENT POPLAR SPECIES

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Abstract – Poplar leaf beetle, *Melasma populi* L. (Coleoptera: Chrysomellidae) is considered a major pest in poplar nurseries in Iran. Planting with a number of poplar species and clones that show relative resistance to poplar leaf beetle can be used as a control measure to alleviate pest damage. The efficiency of these resistant poplar species and clones will in turn increase if they could support the activity of natural enemies of the pest. This study was carried out in the poplar nursery of the Alborz Research Center, Karadj, and aimed to determine levels of attack by the hymenopteran parasitoid *Schizonotus sieboldii* Ratzeburg (Hymenoptera: Pteromalidae) on poplar leaf beetle pupae on seven different poplar species. Large numbers of *Melasma populi* L. pupae that had developed as larvae on one of six different poplar species (*Populus trichocarpa*, *P. deltoides*, *P. euramericana*, *P. simonii*, *P. nigra*, *P. alba* and *P. triplora*) were collected in early May. Between 10 and 38 (mean 28.5) pupae were collected from each poplar species (total n=401) and placed in separate glass jars for rearing under laboratory conditions. The parasitoid was found to emerge only from pupae collected on *P. nigra*. Total parasitism rate of by *Schizonotus sieboldii* on the 144 pupae collected from *P. nigra* was 15.9%. This wasp is a gregarious parasitoid, with up to six adults emerging from each pupa. The reason that the parasitoid attack only pupae collected on *P. nigra* could be attributed to physical or chemical characteristics of poplar species.

Key words: *Melasma populi*, *Schizonotus sieboldii*, Coleoptera, Pteromalidae, parasitoid

Introduction

Many varieties of poplar species and clones are planted in different ecological regions of Iran. A number of insects, fungi, bacteria and viruses inflict damage to poplar and limit poplar plantation in Iran. Among these pests, poplar leaf beetle, *Melasma populi* L. is one of the most important in poplar nurseries. This insect is widely distributed in Iran (Abaii 2000). Adults and all larval instars of the pest feed on leaves of different poplar species and clones and decrease the photosynthesising leaf area of host trees, causing heavy damage to poplar nurseries. Adults that emerge from hibernation can be found on poplar trees from mid April and after oviposition, produce one generation per year. (Sadeghi, unpublished.)

The integrated pest management program for controlling *M. populi* is focused mainly on resistant poplar species and clones as well as using their natural enemies. Laboratory and field studies have been conducted on host preference in *M. populi* and the effect of poplar clones on some biological characteristics of the pest, such as larval development, leaf area consumed by female insects, and adult preference for egg laying sites (Augustin & Levieux 1993; Sadeghi 2000; Sadeghi *et al.* 2000).



Resistance and susceptibility of a few poplar species and clones have been studied to two poplar leaf beetles, *Melasoma populi* and *Chrysomela tremula*. Some of the clones tested were completely susceptible while others were relatively resistant to the pest (Augustin & Levieux 1993). On the basis of laboratory and field studies, black poplar *P. nigra* and hybrid poplar *P. x euramericana* were more preferred by the beetle for feeding and laying egg than *P. simonii* and *P. alba* (Sadeghi *et al.* 2000).

Several insect, fungal and protozoan agents have been reported as natural enemies for the pest. The natural enemies reported for *M. populi* in Turkey were *Schizonotus sieboldii*, *Meigenia dorsalis*, *Meigenia sp.*, *Coccinella saucerotti*, *Chrysopa formosa*, *Leptus sp.*, *Beauveria bassiana*, *Nosema melasomae*, and syrphid species. Among several insect species reported as parasitoids or predators for the poplar beetle, *M. populi*, the pupal parasitoid wasp *S. sieboldii* was reported as the most effective (Zeki & Toros 1990) (Lotfalizadeh & Ahmadi 1997). Parasitism rates of the wasp on *Chrysomela (Melasoma) populi* and *C. tremula* in Turkey were reported to lie in the ranges 14.29-93.15% and 3.57-81% respectively (Zeki & Toros 1990). The parasitism rate of the parasitoid wasp reported on *M. populi* in Fars province, Iran was 76% (Lotfalizadeh & Ahmadi 1997). This parasitoid wasp has been reported as a pupal parasitoid on *M. vigintipunctata* from Bulgaria (Penev & Ovcharov 1992), on *M. populi* and *C. tremula* from Turkey (Zeki & Toros 1990), on *C. tremula* from France (Augustin & Levieux 1993), on *Plagiodra versicolora* from USA (Dowden 1939) and on *Chrysomela lapponica* L. from the Altai region of the CIS (Dolgin 1975). Another species of this genus, *Schizonotus latus* (Walker) is a known parasitoid of *Chrysomela scripta* Fabricius in the USA (Burkot & Benjamin 1979; Burrito & Benjamin 1978).

Several elements, including biotic and abiotic factors, physical and chemical characteristics of plant hosts, and agrotechnical practices etc. are thought to affect the activity of herbivorous insects and their natural enemies. In comparison with studies conducted on other effecting factors on natural enemy activity, a few studies have been already carried out to evaluate the role of host plant on parasitic and predatory arthropods. This study aimed to examine the hypothesis that parasitoid wasp activity on *Melasoma populi* varies among poplar species and clones.

Materials and Methods

This study was carried out in Alborz research center located in the vicinity of Karadj City, Iran. Different poplar species and clones were planted in 1994, including *Populus trichocarpa*, *P. euramericana marilandica*, *P. e.* 561/41, *P. e.* I-214, *P. e. vernirubensis*, *P. simonii*, *P. nigra betulifolia*, *P. n.* 42/78, *P. n.* 63/135, *P. n. turkey*, *P. deltoides* 69/55, *P. d.* 77/51 and *P. triplo*. The poplar trees in our study (1999-2000) were 5 and 6 years old. These trees had poor growing conditions. Twenty-five stands of each poplar species had been planted in five rows in each plot, with one meter spacing between rows and trees. In the early spring of 1999-2000, poplar trees were naturally infected by *Melasoma populi*.

Fluctuation of the poplar leaf beetle population. From early spring of each study year, the number of all developmental stages of the pest were recorded on each poplar clone. In each experimental plot, four poplar trees were sampled weekly. On each tree, four branches (1 from each of north, east, south and west faces of the trunk) were selected at a height of 1.5 meters, each with a length of 150 cm. For each branch, the number of each developing stage of pest was recorded.

Parasitoid wasp: In mid may of 1999, poplar leaf beetle pupae that had completed their immature larval stages on each poplar species were collected separately and placed in ventillated plexiglass jars under natural light conditions in the laboratory. During the pupal period, the temperature of the laboratory varied from 19°C to 27°C. Un-opened pupae were transferred to petri-dishes (20-cm diameter). Emerging parasitoid wasps were recorded separately for each poplar species and clone, and then put into 70° alcohol.

The number of *M. populi* pupae collected on each poplar treatment varied from 11 to 43 depending on the number of pupae present on a single clone.

During the spring of 2000, some poplar leaf beetle pupae were collected weekly from each poplar clone, and parasitoid wasp activity relating to poplar clones was verified. But the wasp parasitism rate in these samples was not be calculated for each poplar clones.

Results

Occurrence of *M. populi* in poplar nurseries

The beetles hibernate as adults under litter and leaves falling the previous year. They appear from early April in poplar nurseries and feed on leaves and buds. At first, the adult beetles attack the poplar species and clones with newly developing leaves or with budburst imminent (as for *P. nigra*). They continue to feed until early May. During this period they may fly to other poplar clones in which leaves develop later. The females deposit eggs from early April till early May. The larvae hatch after an egg development period, and three larval stages develop from mid April to mid May. The pupal period was very short, and occurred mainly at the end of the first ten days in May. A few pupae were observed until mid May. Newly emerged adults appeared from the end of the first ten days of May and can be observed until the end of May. After this period the adults search out hibernation sites under fallen leaves of deciduous trees.

Parasitoid wasp distribution

During this study, the parasitic wasp was collected from *M. populi* pupae in Karadj (Tehran province), Isfahan, Chahar Maha-Bakhtiary, and Markazi provinces. These are the first records from these regions.

Some notes on the biological characteristics of the wasp

Schizonotus sieboldii is a gregarious wasp, with several individuals observed to emerge from each *M. populi* pupa. On the basis of the studies in 2000, the average number of wasps emerging from each *M. populi* pupa was 6. All larval stages of the wasp consume all the internal tissues of the host and pupate in the empty host pupal skin. The pupal stage of the parasitoid lasted 12 days in the laboratory at a mean daily temperature of 19°C.

Parasitism rate

The number of *M. populi* pupae collected on each poplar clone, the number of parasitoid wasp emerging from each group of pupae, and the numbers of *M. populi* pupae dying from causes of mortality other than parasitoid wasp attack in 1999 are shown in table 1.

The total number of *M. populi* pupae collected in 1999 on all poplar clones were 401. From these, 23 *Schizonotus sieboldii* emerged, so the overall parasitism rate was 5.9%. Neither adult beetles nor parasitoid wasps emerged from 13 *M. populi* pupae. These pupae were killed by other unknown factors (probably entomopathogens).



Parasitism rate related to poplar clones

Table 1 shows that this wasp emerged only from the pupae collected on *P. nigra* clones. The number of *M. populi* pupae collected on *P. nigra* clones was 144 and the number of wasps recorded from these pupas were 23, giving a parasitism rate of 15.9%. No wasps emerged from the *M. populi* pupae collected from the other poplar clones. In the year 2000, the relationship between wasp activity and poplar clones was verified, with wasps reared only from pupae collected from *P. nigra* clones.

Table 1 The number of *M. populi* pupae collected on each poplar clone, the number of parasitoid wasps emerging from each group of pupae as well as the number of *M. populi* pupa killed by factors other than parasitoid wasps in 1999

Poplar clones	Number of <i>M. populi</i> pupae collected	Number of emerged parasitoid wasp	Number of <i>M. populi</i> pupae killed by other factors
<i>Populus trichocarpa</i>	33	0	2
<i>P. euramericana</i> <i>marilandica</i>	25	0	1
<i>P. e.</i> 561/41	25	0	4
<i>P. e.</i> I-214	24	0	3
<i>P. e. vernirubensis</i>	23	0	0
<i>P. simonii</i>	38	0	1
<i>P. nigra betulifolia</i>	33	5	0
<i>P. n.</i> 42/78	43	10	0
<i>P. n.</i> 63/135	41	3	0
<i>P. n. turkey</i>	27	6	0
<i>P. deltoides</i> 69/55	23	0	2
<i>P. d.</i> 77/51	11	0	0
<i>P. a.</i> 56/57	23	0	0
<i>P. triplo</i>	32	0	0

Discussion

The parasitism rate found in this study (5.9%) is relatively less than those reported for *S. sieboldii* in Turkey (Augustin & Levieux 1993), and the Shiraz region of Iran (Lotfalizadeh & Ahmadi 1997). The parasitism rate of the wasp on *M. populi* reported in Turkey varied from 14.29 to 93.15% and the parasitism rate reported from Shiraz region of Iran was 76%.

These differences are probably due to several factors:

- 1) Climates of Shiraz and Turkey are different from those of our study site, and the biotic and abiotic factors affecting *S. sieboldii* populations in these sites may differ.
- 2) Other studies have reported the high mortality inflicted by this parasitoid on an alternative poplar leaf beetle host, *M. tremulae* (Augustin & Levieux 1993), and this alternative host is known to occur in poplar nurseries along with *M. populi* in Turkey and several European countries. It is possible that the abundance of this alternative host may influence parasitism on *M. populi*.

- 3) We did not consider the possible existence of beetle and parasitoid host races, which could potentially be associated with poplar clones or species.

The parasitoid wasp was reared only from *M. populi* pupae collected from *P. nigra* clones, and was not found from pupae collected from the other poplar clones. This is the first report of this phenomenon concerning *S. sieboldii*. This phenomenon has already been reported for other host plants, herbivorous insects and their natural enemies, and is considered relevant to the study of tritrophic insect-plant interactions (Vet *et al.* 1992), indirect plant defense (Dicke 1994), and potential mutualism between plants and natural enemies in pest exclusion (Takabayashi *et al.* 1995). In addition to several biotic and abiotic factors that influence the activity of parasitoids or predatory insects, physical and chemical characteristics of host plants act as attractant or inhibitory factors for natural enemies. Thus it is probable either (a) that *P. nigra* clones have genetic characteristics that can produce special infochemicals for attracting *S. sieboldii* or (b) that certain physical characteristics of *P. nigra* clones attract them. Important infochemical or volatile organic compounds have been identified and isolated from several plants (Dicke *et al.* 1990; Finidori-logli *et al.* 1996; Mattiacci & Dicke 1995; Takabayashi *et al.* 1995; Turlings *et al.* 1991).

Higher parasitism rates of the wasp on *M. populi* feeding on *P. nigra* clones can be explained by the facts that: 1) while *P. nigra* and *P. alba* that are native species for Iran, the others examined are exotic (*P. deltoides*, *P. euramericana*, *P. simonii*, *P. triplo* and *P. trichocarpa* clones); 2) The poplar leaf beetle, *M. populi* has a long history of herbivory on black poplar in Iran (Abaii 1984; Farahbakhsh 1961), and 3) though this parasitoid was reported for first time only in 1997 (Lotfalizadeh & Ahmadi 1997), beetle and wasp and sympatric and probably have a long coevolutionary history. The tritrophic relationship with sympatric poplar is also probably relatively ancient formed. For *P. alba*, although this species is native, we found no parallel tritrophic relationship because this poplar species is not a good host for *M. populi* (Sadeghi *et al.* 1997).

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PART 8

Biological Control



ROLE OF BRACONIDAE (HYMENOPTERA) IN LIMITATION OF LEPIDOPTERA CABBAGE PESTS POPULATIONS IN ROMANIA

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Abstract – The complex of parasitoids associated with lepidopterous cabbage pests in Romania is given. Ten primary Braconidae parasitoids are identified: *Cotesia glomerata* (L.), *C. plutellae* (Kurd.), *C. rubecula* (Marsh.), *C. rubripes* (Hal.), *C. ruficrus* (Hal.), *C. spurius* (Wesm.), *Apanteles appellator* Tel., *Macrocentrus collaris* (Spin.), *Microchelonus contractus* (Nees), *Microgaster mediator* Hal. Abundance, constancy, dominance, the biocenotic affinity and the contribution of each species in limiting populations of lepidopterous pests are analyzed.

Key Words: *Plutella xylostella*, *Pieris brassicae*, *Pieris rapae*, *Mamestra brassicae*, cabbage, braconid wasp, biological control

Introduction

The braconid wasps represent the second most numerous family of parasitic Hymenoptera. Most of them use as a host many lepidopterous species being true natural regulators of many pests. Over 2000 braconid species are known in Europe (Tobias 1976; Tobias 1986; Belokobylskij & Tobias 2000), but the real number could be several times more. Braconids – parasitoids of cabbage pests in Romania have been studied by Lăcătușu, Tudor & Borcan (1986), Mustață (1973, 1992), Mustață & Andriescu (1972-1973), Mustață & Costea (2000), Mustață & Lăcătușu (1973). Comparing to other countries which introduced and tried to acclimatized parasitoid species of dangerous Lepidoptera in the cabbage crops, in Romania parasitoids that limit the populations of *Plutella xylostella* L., *Pieris brassicae* L., *Pieris rapae* L. are so abundant that we cannot talk about the necessity of their laboratory mass-rearing and releasing them into the agroecosystems but only about their protection (Andriescu, Saucinițianu *et al.* 1974-1975; Mustață 1973; Mustață & Andriescu 1972-1973; Mustață 1992).

The goal of our research was to observe how parasitoid complexes limit lepidopteran pests populations on the cabbage crops. Numerous experiments have shown that pest populations often flourish in absence of predators and parasitoids, often killed by the pesticide applications used to control the pest. Chemical pesticides affect more the beneficial insects than the pests themselves, because they are more sensitive.

Materials and Methods

Research was carried out in 1999-2000 within 24 sites in South Eastern Romania. 3067 larvae and pupae of *Plutella xylostella* L., *Pieris brassicae* L., *Pieris rapae* L., *Mamestra brassicae* L.

were collected. The investigations revealed a complex of Braconidae and other groups of parasitoids that limiting dangerous lepidopteran pests.

Collectings were made not only in chemical treated crops but also in crops situated in the neighborhood of natural ecosystems or in the non-chemical treated control areas. In chemical treated crops the pests survived after treatments. Ten species of Braconidae (primary parasitoid) and 7 species of secondary parasitoid agents were reared.

In order to clarify the role of each species in the limitation of the host populations, we have made synecological analysis to establish the abundance, the constancy, the dominance and the contribution of each parasitoid species in limiting dangerous Lepidoptera pest populations on cabbage crops.

Results and Discussion

The investigations revealed a complex of 10 braconid species that limit *Pieris brassicae* L., *Pieris rapae* L., *Plutella xylostella* L., and *Mamestra brassicae* L. populations (Fig. 1).

Five primary braconid species and 7 secondary parasitoids have been found. Four new host-parasitoid relationships were established for Romania for the first time: *Microchelonus contractus* on *Plutella xylostella*; *Mesochorus anomalus* on *Cotesia plutellae*, *Cotesia rubecula* and *Apanteles ruficrus*; *Mesochorus orbitales* on *Cotesia rubecula* and *Cotesia plutellae*; *Mesochorus facialis* on *Apanteles ruficrus* and *Cotesia plutellae* (Fig. 1).

1655 larvae and pupae of *Plutella xylostella* were collected which from 1043 were parasitized by ichneumonids and braconids, particularly 53,69% were infested by braconids (Table 1). Six braconid species were reared from *P. xylostella* during 1999-2000, which from *Cotesia plutellae* had the highest (64,1%) and *Microchelonus contractus* – the lowest (0,89%) parasitization rate (Table 1).

Referring to *Pieris brassicae*, from 1008 collected larvae and pupae, 50,4% were parasitized, which from 75,2% were infested by braconids. From 4 braconid species reared from *Pieris brassicae*, parasitization rate varied from 55,2% in *Cotesia glomerata* to 3,1% in *Apanteles spurius* (Table 1).

From 377 collected larvae and pupae of *Pieris rapae* 63,9% were parasitized, which from 70,1% by *Cotesia rubecula* (Table 1).

From 81 collected larvae and pupae of *Mamestra brassicae*, 33,3% were parasitized, which from only 11,1% by braconid species (Table 1). As one can see, braconids have a high efficiency in the regulation of Pieridae pest populations: around 75,2% in *Pieris brassicae*, 70,1% in *Pieris rapae*, 53,69% in *Plutella xylostella*, and only 11,1% in *Mamestra brassicae*. Ichneumonid wasps and tachinid flies caused the rest parasitization (Diptera: Tachinidae). The interrelations between the braconid species that limit dangerous Lepidoptera pests of cabbage crops are shown in Fig. 1.

Between the dominant species, *Cotesia plutellae* is the first, followed by *Cotesia rubecula*, *Cotesia glomerata*, *Apanteles rubripes* and *Apanteles appellator*. Other braconid species play a minor role in reducing host populations (Table 2).

In Table 2 species are listed according to their abundance. The highest value assigned to *Cotesia plutellae* with 359 specimens, followed by *Cotesia rubecula* with 290 specimens and *Cotesia glomerata* with 211 specimens. *Microgaster mediator* and *Macrocentrus collaris* assigned the lowest values with only two or one specimens each (Table 2).



Table 1 The limitation of dangerous Lepidoptera by braconids in South-Eastern Romania (1999-2000)

Total hosts		Braconid parasitoids													
		Parasitoids		Total	%	Apanteles appellator Tel.	Cotesia glomerata L.	Cotesia plutellae Kurd.	Cotesia rubecula Marsh.	Apanteles rubripes Hal.	Apanteles ruficrus Hal.	Apanteles spurius Wesm.	Macrocentrus collaris Spin.	Microchelonus contractus Nees.	Microgaster mediator Hal.
		Total	%												
Plutella xylostella L.															
1655	1043	63,02	560	53,69	64 11,42		359 64,1	34 6,07	46 8,2	52 9,3				5 0,89	
Pieris brassicae L.															
1008	508	50,4	382	75,2		211 55,2		87 22,8	72 18,8			12 3,1			
Pieris rapae L.															
377	241	63,9	169	70,1				169 100,0							
Mamestra brassicae L.															
81	27	33,3	3	11,1									1 33,3		2 66,6
Total															
3121	1819	58,28	1114	61,24	64 5,7	211 18,9	359 32,2	290 26,03	118 10,6	52 4,6	12 1,07	1 0,09	5 0,45	2 0,18	

Table 2 The synecological analysis of the braconid species in the lepidopteran pest populations

Species	Abundance	Dominance	Constancy	Index of ecological significance			
<i>Cotesia plutellae</i>	359	26,64	D ₄	62,5	C ₃	18,5	W ₅
<i>Cotesia rubecula</i>	290	23,94	D ₄	62,5	C ₃	14,9	W ₅
<i>Cotesia glomerata</i>	211	17,42	D ₄	50	C ₂	8,7	W ₄
<i>Apanteles rubripes</i>	128	10,56	D ₄	20,83	C ₁	2,18	W ₃
<i>Apanteles fuliginosus</i>	87	7,18	D ₄	20,83	C ₁	1,49	W ₂
<i>Apanteles appellator</i>	64	5,28	D ₄	29,16	C ₂	1,51	W ₂
<i>Apanteles ruficrus</i>	52	4,29	D ₃	20,83	C ₁	0,89	W ₂
<i>Apanteles spurius</i>	12	0,99	D ₁	12,5	C ₁	0,12	W ₂
<i>Microchelonus contractus</i>	5	0,41	D ₁	12,5	C ₁	0,05	W ₁
<i>Microgaster mediator</i>	2	0,16	D ₁	25	C ₁	0,04	W ₁
<i>Macrocentrus collaris</i>	1	0,08	D ₁	4,16	C ₁	0,003	W ₁
TOTAL	1211						

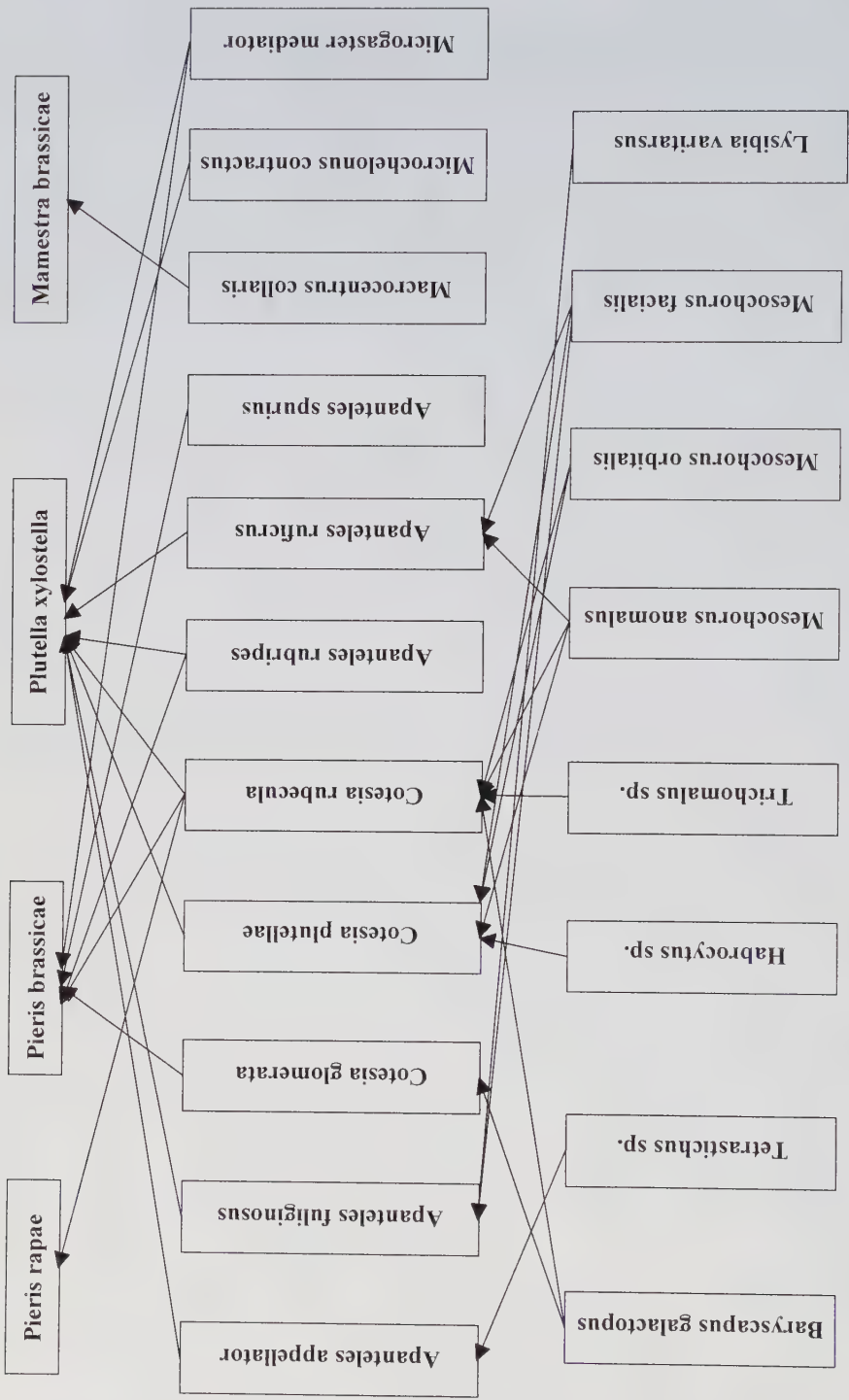


Figure 1 Parasitoid complexes of the dangerous lepidopteran species



To appreciate the importance of braconid parasitoids presence within the complex, we analyzed their constancy what indicates the contribution of a species within the biocenosis. We can deduce that *Cotesia plutellae* and *Cotesia rubecula* are act as a constant parasitoids and these species were found in all cabbage fields in South Eastern Romania during 1999-2000, wherever Lepidoptera attacks cabbage.

The index of ecological significance shows eloquently the position of each species in the complex. In this respect *Cotesia plutellae* and *Cotesia rubecula* have the highest values, followed by *Cotesia glomerata* with W4 and nine other species with W3, W2, and W1.

Conclusions

Studies were made in 24 localities in South-Eastern Romania in 1999 –2000, during which 3067 larvae and pupae of *Plutella xylostella* L., *Pieris brassicae* L., *Pieris rapae* L., and *Mamestra brassicae* L. were collected. Ten species of primary braconid wasps and 7 species of secondary parasitoids were reared from these pests. Four new host-parasitoid relationships were found for Romania. Synecological analysis concerning the role of these parasitoids has been done.

Our researches showed that the role of braconid species in limiting the dangerous Pieridae populations of cabbage crops is important and can reach 75.0%, while in the case of *Plutella xylostella* – 53.0%.

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PRIMARY AND SECONDARY PARASITISM IN THE *CAMERARIA OHRIDELLA* COMPLEX (LEPIDOPTERA: GRACILLARIIDAE)

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Abstract – Some biological aspects of 4 eulophid parasitoids of the horse chestnut leafminer, *Cameraria ohridella* Deschka & Dimic have been investigated in this study. The most abundant species was *Minotetrastichus frontalis* (Nees), it parasitized all larval instars of *C. ohridella* except the first one and could also be found on pupae. The spinning stages of the moth were attacked most frequently, in these cases gregarious development could be observed. *Pnigalio agraulis* Wlk. was found to develop as a solitary and primary parasitoid only. The species attacked the leafminer earlier and therefore seems to favour the last feeding instar of the moth. *C. ohridella* pupae were not parasitized. *P. agraulis* itself often became victim of the facultatively hyperparasitic *M. frontalis*. As member of the subfamily Entedoninae *Chrysocharis nephereus* Wlk. develops endoparasitic in leafminer larvae. In contrast to the two species mentioned above, *C. nephereus* attacked the leafminer in a very short period of time, which strongly suggests that it parasitized the spinning stages only. *Closterocerus trifasciatus* also developed endoparasitically in late larval instars and in pupae of *C. ohridella*. Especially males of the species showed a strong preference for hyperparasitic development on other endoparasites of the moth, e.g. *Chrysocharis* spp.

Key words: *Cameraria ohridella*, leafminer, horse chestnut, parasitoid, host preference

Introduction

The horse chestnut leafminer, *Cameraria ohridella* Deschka & Dimic, has rapidly spread over large parts of Europe in the last years and is still expanding its area. Due to the high population densities, the damage on the leaves of *Aesculus hippocastanum* L. caused by feeding larvae is obvious and the leafminer attracted much publicity especially in urban areas, where horse chestnuts are planted as ornamental trees. One of the main reasons for the continuous heavy infestation may be due to the inefficiency of natural control mechanisms in Europe. As natural enemies usually play an important role in the control of a leafminer population, research work of the last years was focussed on the parasitoids affecting *C. ohridella*.

More than 20 species of parasitic Hymenoptera have already been reared from preimaginal stages of the horse chestnut leafminer in Europe, Horváth *et al.* (2001) summarized the most important published parasitoid lists. With a few exceptions parasitoids belong to the superfamily Chalcidoidea, the chief component being the Eulophidae with about 15 species. Since *Cameraria ohridella* has been introduced into Europe, it is no wonder that specialists cannot be found in the spectrum, all the parasitoids are polyphagous and also occur on other related leafminer species. They attack preferably larvae or sometimes pupae of the moth, egg parasitoids could not be found until now.

The present paper deals with some biological details of four eulophid species occurring regularly on the horse chestnut leafminer. The aim of the study was to find out the favoured



leafminer stages attacked by the parasitoids and to detect possible hyperparasitic relations between the different species.

Materials and Methods

Enclosure experiments were carried out in a small horse chestnut stand south of Vienna in 1998, where trees have never been sprayed against the leafminer and suffered heavy attack by the moth without interruption since 1995. After an egg laying period of ten days for the leafminer, 300 leaves were carefully cleaned from spiders and insects and enclosed in a gaze bag. For each preimaginal stage the bags of 30 leaves were removed for 10 days to expose larvae for parasitism. After exposure leaves were enclosed again and left on the trees until first adult moths emerged.

Different larval instars were determined by measuring the size and observing the shape of the mines. As this method sometimes does not allow exact statements and different instars occurred on one leaf, samples were classified in categories referring to the most abundant larval (or pupal) stage. Another 30 leaves never enclosed were taken as control from the same trees. All samples were stored in a climatic chamber (25°C, 65% relative humidity, 16,5 h daylight) and parasitoids determined after two months of emergence.

Results

Eight species of parasitic Hymenoptera in total were reared from the leafminers, the following four species from the superfamily Chalcidoidea occurred in larger numbers and gave reasonable results.

Minotetrastichus frontalis (Nees) (Eulophidae: Tetrastichinae) was the most abundant species, it occurred in all samples except the first and the second one with eggs and small larval instars. The sample most frequently parasitized was the fifth with predominantly spinning stages of the moth. *M. frontalis* could also be reared from the last sample, where only leafminer pupae occurred in the mines. The third and fourth sample (feeding larvae) produced predominantly males whereas females dominated all the other samples (spinning stages and pupae). Gregarious development occurred in late samples (from the fourth onwards). Facultative hyperparasitism was observed on other ectoparasites of the horse chestnut leafminer.

Pnigalio agraulis (Walker) (Eulophidae: Eulophinae) attacked *C. ohridella* earlier than *M. frontalis*. Most specimens emerged from the fourth sample (mainly last feeding larval instar). From the fifth sample (predominantly spinning stages) only a few specimens could be reared. The species did not occur in samples with pupae. *P. agraulis* developed only solitary and as primary ectoparasite of the moth.

Chrysocharis nephereus (Walker) (Eulophidae: Entedoninae) attacked the leafminer only in a short period of time in contrast to the two species mentioned above. More than 90% of all specimens were found in the fifth sample (mainly spinning stages). In general, the number of *C. nephereus* individuals emerged from enclosed samples ($n = 104$) was significantly higher than the number reared from the control ($n = 31$).

Closterocerus trifasciatus Westwood (Eulophidae: Entedoninae) like *M. frontalis* could be found in every sample from the third onwards, a distinct preference for a certain host stage could

not be improved. The number of individuals emerging from enclosed leaves was very small ($n = 11$) compared to the control ($n = 29$).

Discussion

For interpretation of the results it is important to note that the preimaginal stages of the leafminer could not be separated exactly in this investigation (see description of method). Therefore the classification of the samples only represents the real developmental stage for the majority of the preimaginal stages in the leaves but is not guilty for the total of *C. ohridella* per sample. Nevertheless the data gained reveal some interesting details on the described chalcids parasitizing the horse chestnut leafminer.

Minotetrastichus frontalis has shown high flexibility with attacking hosts from at least the third larval instar to the pupal stage. In this ectoparasitic species the host stage killed is the same as attacked by the ovipositing female, leafminer larvae therefore do not develop after being parasitized. The disadvantage of small host stages is compensated by some reproductive strategies of the parasitoid. The size of the emerging adult varies with the size of the host. Ovipositing female parasitoids in general are able to discriminate between small hosts on which it lays unfertilized male eggs and larger hosts on which fertilized female producing eggs are laid (Askew & Shaw 1979). Therefore (on average smaller) males dominated in earlier samples whereas more females emerged from the later ones. As *M. frontalis* is a gregarious species the host quality also influences the number of eggs per host laid. While up to seven parasitoids could be found feeding on spinning stages, earlier instars are more often parasitized by only one or two individuals.

Pnigalio agraulis was found to attack the leafminer earlier than *M. frontalis*, preferably the last feeding stages of the moth. There are only suggestions why the spinning stages were not parasitized to a greater extent. Former investigations have shown that mainly male *P. agraulis* emerged about a week earlier from mines of the first generation of the moth than most of the other parasitoids (Grabenweger & Lethmayer 1999), which stands in concordance to the results gained in this study. *P. agraulis* as relatively large species may also be able to paralyse the last feeding stage, which shows strong defensive behaviour, more easily. In addition, the parasitoid often itself becomes victim of *M. frontalis*, which predominantly searches for spinning stages. This facultative hyperparasitism may have had strong influence on the results.

In contrast to *P. agraulis*, *C. nephereus* seems to be rather fixed on the spinning stages of the moth. Despite of their endoparasitic development, *Chrysocharis* spp. seem to paralyse the host larvae and therefore prevent their further development. Consequently, they attack only late host stages (Askew & Shaw 1979; Mey 1993). In concordance with the present data a similar development strategy can be expected for *C. nephereus* on the horse chestnut leafminer. The species attacks the spinning stages of the moth and presumably paralyses the larvae in the same stadium. Seven *C. nephereus* (out of a total of 104 individuals) reared from other samples can be neglected considering inexact division of the developmental stages.

Regarding the parasitoid spectrum, enclosure experiments had an interesting side effect. The gaze bags did not only protect the moth larvae from being parasitized but also prevented hyperparasitism, which strongly influenced the abundance of two parasitoid species. Whereas *C. nephereus* was found in significantly higher numbers in the enclosed samples, much more



Closterocerus trifasciatus emerged from the control. The endoparasitic *C. trifasciatus* larvae were observed to emerge from the leafminer remains and to pupate free several millimetres from the host. In many cases, the impression that they developed on *C. ohridella* deceives. The real host especially of the males from this species often is another endoparasitoid of the leafminer on which *C. trifasciatus* feeds as a hyperparasitoid. Similar observations were made by Askew & Shaw (1979), who worked on parasitoids attacking *Phyllonorycter* larvae. In the horse chestnut leafminer spectrum, *C. nephereus* was the most important primary endoparasitic species. Protected from the gaze bags, lots of specimens could easily complete development, whereas in the never enclosed control *C. nephereus* was parasitized regularly by *C. trifasciatus*. In the never enclosed control the species nearly lost half of its share of the spectrum whereas *C. trifasciatus* increased in importance proportionally.

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THE PARASITISM OF THE HORSE CHESTNUT LEAFMINING MOTH (*CAMERARIA OHRIDELLA*) IN AUSTRIA

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Abstract – The parasitoid complex of the horse chestnut leafmining moth, *Cameraria ohridella*, was examined in Vienna and Lower Austria since autumn 1996. During this investigation period a total of 16 species of parasitoids was found on *C. ohridella* belonging to the Hymenopteran suprafamilies Chalcidoidea and Ichneumonoidea, the latter being rather unimportant. Within these chalcidoid wasps the Eulophidae are the chief group with the 2 most abundant species *Pnigalio agraulis* Wlk. and *Minotetrastichus frontalis* (Nees). All these parasitoid species are quite common on different leafmining insects in Europe, polyphagous and ecto- or endoparasitic. It seems that an adequate adaptation of the local parasitoids still not exists until now having only very low levels of parasitism compared to other leafmining moths and referring to the heavy infested trees. Additionally, it is expected that there will be no significant increase in parasitism in the near future following the tendencies of the last years.

Key words: *Cameraria ohridella*, leafmining, moth, parasitoid, Chalcidoidea, Eulophidae, Ichneumonoidea

Introduction

During the last years the horse chestnut leafmining moth, *Cameraria ohridella* Deschka & Dimic (Lepidoptera: Gracillariidae), occurred with mass infestation on horse chestnut trees (*Aesculus hippocastanum* L.) almost in whole Europe. Several studies have been carried out on the natural enemy-complex of the moth and results showed that the most important natural enemies are parasitic wasps. In the studies of Deschka (1995), Lethmayer & Grabenweger (1997), Stolz (1997) and Grabenweger & Lethmayer (1999) first results on the parasitoids of *C. ohridella* in Austria are demonstrated. In this paper further investigations on the parasitoids of the horse chestnut leafmining moth are presented showing the species composition and the tendency of natural parasitization since 1996.

Materials and Methods

Leaf samples have been taken from infested horse chestnut trees in Vienna (Prater) and Lower Austria (Stein/Krems) from autumn 1996 to autumn 2000. These infested leaves were collected from the lower branches of the trees in spring, summer and autumn respectively for every of the 3 moth generations. Samples were taken every week from May to October in 1997 and only for 3 following weeks in spring, summer and autumn in the years 1998 to 2000.

Two methods have been used to obtain the parasitoid species and the rate of parasitism – the rearing method and the dissection method. For the rearing method (see also Grabenweger &



Lethmayer 1999) a total of 90 infested leaves were collected per sample date, the larvae and pupae of *Cameraria* were counted and always 10 leaves were put together in one box for hatching. After several weeks the boxes were opened and the emerged adult parasitoids were taken for determination. For the dissection method (only in 1998 and 1999) 500 mines per sample were opened and examined for parasitized larvae and pupae.

Results

Parasitoid spectrum

A total of 16 species was obtained on *C. ohridella*. Most of these species belong to the Hymenopteran superfamily Chalcidoidea with the families Pteromalidae, Eupelmidae and Eulophidae including the most species and individuals. Only few are Ichneumonoidea with the families Ichneumonidae and Braconidae (Table 1).

Table 1 The parasitoid spectrum of *Cameraria ohridella* from investigation sites in Vienna and Lower Austria (Austria)

Superfamily	Species
Ichneumonoidea	<i>Itoplectis alternans</i> (Gravenhorst)
	<i>Scambus annulatus</i> (Kiss)
	<i>Colastes braconius</i> Haliday
	<i>Gelis spurius</i> (Foerster)
Chalcidoidea	<i>Minotetrastichus frontalis</i> (Nees)
	<i>Pnigalio agraulis</i> Walker
	<i>Closterocerus trifasciatus</i> Westwood
	<i>Chrysocharis nephereus</i> Walker
	<i>Cirrospilus vittatus</i> (Walker)
	<i>Cirrospilus viticola</i> (Rondani)
	<i>Cirrospilus pictus</i> (Nees)
	<i>Pteromalus</i> cf. <i>semotus</i> Walker
	<i>Baryscapus nigroviolaceus</i> (Nees)
	<i>Pediobius saulius</i> Walker
	<i>Pnigalio pectinicornis</i> (Linnaeus)
	<i>Eupelmus urozonus</i> Dalman

They are all polyphagous on different leafmining insects and none is specialized on *C. ohridella*. There are 2 dominating species which are present on every site and at every time of sampling: *Minotetrastichus frontalis* and *Pnigalio agraulis*. The endoparasitic wasp *Closterocerus trifasciatus* also appears regularly, but only in low abundance. Species of *Chrysocharis* and *Cirrospilus* and *Pteromalus* cf. *semotus* also occur more or less regularly; and the species *Baryscapus nigroviolaceus*, *Pediobius saulius*, *Pnigalio pectinicornis* and *Eupelmus urozonus* have been found only in a few number of samples with very few individuals. The group of Ichneumonoids is not very important for *Cameraria* having only few individuals in all samples.

Rate of parasitism

In Fig. 1 and Fig. 2 the preliminary results (results from 1996 to 1999) of the parasitization are shown having obtained with two methods (rearing and dissection). On both sites the parasitization level is very low, on average only 5 to 20%, only few samples are over 20% or even below 5%. In 1997 and 1998 a maximum of parasitism has always been reached on both sites during summer whereas a decrease was in spring and autumn. In the following year (1999) there was a very low parasitization level in general, except in Lower Austria having there an increase in autumn. The same tendencies are observed with both methods.

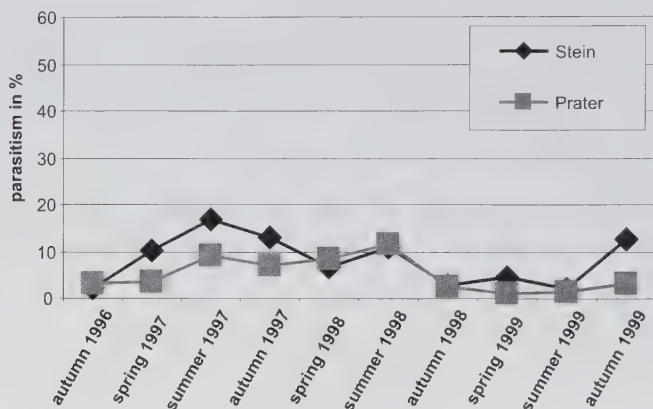


Figure 1 The level of parasitism (in %) of *Cameraria ohridella* from infested horse chestnut trees in Vienna (Prater) and Lower Austria (Stein) from autumn 1996 to autumn 1999 (results obtained with the rearing method)

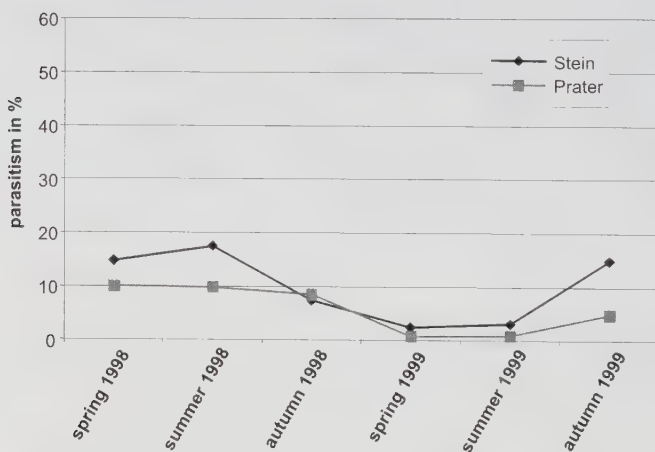


Figure 2 The level of parasitism (in %) of *Cameraria ohridella* from infested horse chestnut trees in Vienna (Prater) and Lower Austria (Stein) from spring 1998 to autumn 1999 (results obtained with the dissection method)

Discussion

The obtained parasitoid spectrum correspond with the results from other studies on the parasitoids of *C. ohridella* (Deschka 1995; Stolz 1997; Hellrigl 1998; Balázs & Thuróczy 2000; Moreth *et al.* 2000). The eulophid wasps are also the most important parasitoids of *C. ohridella* and *Minotetrastichus frontalis*, *Pnigalio* spp. and *Chrysocharis* spp. belong to the most abundant species.

In comparison to other leafmining moths in Europe, e.g. *Phyllonorycter platani*, *Ph. robiniellus*, *Ph. blancardella*, the parasitoid spectrum of *Cameraria* is also quite common having 15 to 20 Chalcidoids, 1 to 3 Ichneumonoids and 2 dominating species (Maier 1984; Casas & Baumgärtner 1990; Mey 1991; Gibogini *et al.* 1996). Furtheron, this study shows that the moth also has larval and pupal parasitoids, mainly polyphagous ectoparasitoids and no specialists. But there is one great difference. The level of parasitism of other leafminers is up to 50% (Delucchi 1958; Askew & Shaw 1979) whereas that of *Cameraria* is much lower. With reference to the results of the last years there was no significant increase recognizable and it will not be expected in the near future.

Nevertheless, it is very important to mention to take care with comparing rates of parasitism from different studies because the results are depending from the time of sampling and especially from the method of evaluation.

Until now, there is no reason known for this low parasitization. It seems that there is still no sufficient adaptation of the parasitoids or maybe the reason is the host-plant, the horse chestnut tree, itself. On the one hand the horse chestnut tree is not native in Austria, on the other hand maybe the shape and morphology or the secondary substances of the leaves have an influence on the parasitoids.

In general, the parasitism is depending from several factors. An important factor is the location, on the one hand the macro- and especially the microclimate and on the other hand the surrounding vegetation of the horse chestnut trees. The more diverse the vegetation is around the tree the more parasitoid species occur. The time of the year respectively the developing stage of the moth has a great effect on the occurrence of the parasitoids. Not to forget the interactions between the parasitoids themselves, like hyperparasitism (Grabenweger, *in prep*).

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PARASITIDS OF HORSE CHESTNUT LEAF MINER *CAMERARIA OHRIDELLA* DESCHKA ET DIMIC, 1986 (LEPIDOPTERA: GRACILLARIIDAE) IN HUNGARY

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Abstract – Authors give a report on the results of a nationwide survey of hymenopteran parasitoids of horse chestnut leaf miner (*Cameraria ohridella*) in 1996-2000. In each county 2x100 pupal chambers were cut out from infested leaves of common horse chestnut (*Aesculus hippocastanum*) then the mines were placed in cage in laboratory. The reared parasitoids were identified. *Minotetrastichus frontalis*, *Pnigalio pectinicornis*, *Closterocerus trifasciatus* and *Pediobius saulius* were the most frequent chalcidoid species. The studies in different habitats show that the dominant parasitoids of closely related leaf miners occurring on fruit crops have found and accepted as host the pest new in Hungarian fauna. Intensity of establishment and richness in species of parasitoids mainly depend on the diversity of environment.

Key words: *Cameraria ohridella*, Gracillariidae, Chalcidoidea, Braconidae, parasitoids

Introduction

In the early '90s a small moth appeared in the focus of interest of the European plant protection researchers. This was a new pest of horse chestnut. The horse chestnut leaf miner (*Cameraria ohridella*) was found in Macedonia in 1984 (Deschka & Dimic 1986).

The first occurrence of lepidopteran pest in Hungary was recorded in the southern part of county Baranya, close to the Croatian border in July 1991. This insect spread rapidly throughout Hungary. Since 1994 the moth has caused severe infestation on street trees, in parks and green areas of housing estates. In 1996 the pest was present in all counties of the country.

In Macedonia, Deschka and Dimic found two parasitoid species belonging to the family Chalcididae in the summer generation of *Cameraria ohridella*. In Upper Austria the role of parasitoids did not have significant role in the regulation of populations of *Cameraria ohridella* (Puchberger 1990). In the western part of Hungary 2,8% of the overwintering generation was parasitized by eulophid species in 1995, while in Budapest parasitism rate of overwintering pupae was as high as from 65 to 70% in 1996/1997 (Reider Saly *et al.* 1999).

Materials and Methods

The Hungarian Plant Protection Organization has carried out a nationwide survey of parasitoids of *Cameraria ohridella* since 1996. From the autumn 1996 the Plant Protection and Soil Conservation Service of Budapest, since 1997 the services in all counties have participated in the

study. The entomologists collected common horse chestnut (*Aesculus hippocastanum*) leaves infested with *Cameraria ohridella*. In each county 2x100 pupal chambers were collected on each location. Then the mines were cut out and were placed in cage in laboratory. After the parasitoids emerged, the adults were sent for identification in small vials to the Systematic Parasitoid Laboratory. In 1998 the collected and cut-out mines were put in small vials and sent to Systematic Parasitoid Laboratory. The vials were closed with cotton-wool cork. The study was done both on the overwintering and summer generations. The Research Institute for Plant Protection made a survey to study the regulating role of native parasitoids of other leaf miners (viz. families Gracillariidae, Lyonetiidae, Nepticulidae) on horse chestnut leaf miner. The studies were done in nine locations in Hungary. The habitats of them were different, such as street trees, solitaire trees in park, typical inner city parks, and in ecologically rich environments, such as park of castle. In some localities the horse chestnut trees were protected against *Cameraria ohridella* while the others were without chemical control. During the season the infested leaves were collected and the reared parasitoids were identified.

All chalcidoid species were identified by Dr. Csaba Thuróczy, and braconids by Dr. Jenő Papp.

Results

Twenty three parasitoid species were reared from *Cameraria ohridella* in Hungary:

Chalcidoidea	<i>Sympiesis gordius</i> (Walker, 1839)
Eulophidae	
<i>Aprostocetus</i> sp.	Eupelmidae
<i>Baryscapus nigroviolaceus</i> (Nees, 1834)	<i>Eupelmus urosonus</i> Dalman, 1820
<i>Baryscapus</i> sp.	<i>Eupelmus vesicularis</i> (Retzius, 1783)
<i>Chrysocharis pentheus</i> (Walker, 1839)	
<i>Cirrospilus pictus</i> (Nees, 1834)	Pteromalidae
<i>Cirrospilus viticola</i> (Rondani, 1877)	<i>Mesopolobus</i> sp.
<i>Cirrospilus vittatus</i> Walker, 1838	<i>Pteromalus semotus</i> (Walker, 1834)
<i>Cirrospilus</i> sp.	<i>Pteromalus</i> sp.
<i>Closterocerus trifasciatus</i> Westwood, 1833	
<i>Minotetrastichus frontalis</i> (Nees, 1834)	Ichneumonoidea
<i>Neochrysocharis</i> sp.	Braconidae
<i>Pediobius saulius</i> (Walker, 1839)	<i>Colastes flavitarsis</i> Thomson, 1891
<i>Pediobius</i> sp.	<i>Colastes vividus</i> Papp, 1975
<i>Sympiesis sericeicornis</i> (Nees, 1834)	<i>Macrocentrus</i> sp.

In 1996/1997 a total of 16 parasitoid species were identified in the overwintering pupae of *Cameraria ohridella*, belonging to 3 families (Table 1). The average parasitism of overwintering generation was low in the country. But there were considerable differences in the particular counties. The highest parasitism level was in Budapest: 65-70%. The two summer generations were parasitized by 11 chalcidoid species. *Minotetrastichus frontalis*, *Pnigalio pectinicornis* and *Pediobius saulius* were the most abundant species. *Baryscapus* sp., *Chrysocharis pentheus*, *Minotetrastichus frontalis*, *Pediobius saulius*, *Sympiesis sericeicornis* and *Pnigalio pectinicornis* were present in both overwintering and summer generations, while *Chrysocharis* sp. only in



summer generations. The polyphagous parasitoids of native leafminers (*Phyllonorycter blancardella*, *Phyllonorycter corylifoliella*, *Leucoptera malifoliella*, *Nepticula malella*) were recovered from pupae of *Cameraria ohridella*. These parasitoids have significant role in regulating the pest populations of fruit crops in Hungary.

Table 1 Parasitoid species emerged from the pupal chambers of *Cameraria ohridella* in Hungary in 1996-1997

Parasitoid species	County		
	overwintering generation	1 st summer generation	2 nd summer generation
<i>Aprostocetus</i> sp.	Budapest		
<i>Baryscapus</i> sp.	Budapest		Budapest
<i>Baryscapus nigroviolaceus</i>			Budapest
<i>Chrysocharis pentheus</i>	Budapest	Szabolcs-Szatmár-Bereg	Budapest
<i>Chrysocharis</i> sp.			Budapest
<i>Cirrospilus pictus</i>	Budapest		
<i>Cirrospilus vittatus</i>	Budapest		
<i>Cirrospilus viticola</i>	Budapest		
<i>Closterocerus trifasciatus</i>	Budapest		Budapest
<i>Eupelmus urosonus</i>	Budapest		Budapest
<i>Mesopolobus</i> sp.	Budapest		
<i>Minotetrastichus frontalis</i>	Budapest, Békés, Csongrád, Szabolcs-Szatmár-Bereg, Zala	Bács-Kiskun	Budapest, Bács-Kiskun, Heves, Szabolcs-Szatmár-Bereg
<i>Neochrysocharis</i> sp.			Budapest
<i>Pediobius saulius</i>	Budapest		Budapest
<i>Pnigalio pectinicornis</i>	Budapest, Somogy, Szabolcs-Szatmár-Bereg		Budapest
<i>Pnigalio</i> sp.	Budapest		
<i>Pteromalus semotus</i>	Budapest		
<i>Pteromalus</i> sp.	Budapest		
<i>Sympiesis sericeicornis</i>	Budapest		Budapest

In 1997/1998 a total of 11 chalcidoid species were found in the overwintering generation (Tables 2 and 3). The average of pupal parasitism was 6.7%. Parasitisation data were significant in Budapest, and counties Békés, Csongrád and Tolna. Parasitism levels were insignificant in the northern and eastern counties viz. Nógrád, Heves, Borsod-Abaúj-Zemplén, Hajdú-Bihar, and Szabolcs-Szatmár-Bereg. Out of the frequent species, *Minotetrastichus frontalis*, *Pediobius saulius*, *Pnigalio pectinicornis*, and *Closterocerus trifasciatus* were present in 7, 6, 5 and 5 counties, respectively. The most parasitoid species were collected in counties Békés and Csongrád, 7 and 4, respectively. The most abundant species were *Pnigalio pectinicornis*, *Minotetrastichus frontalis*, *Pediobius saulius*. In the first summer generation 10, in the second generation 7 parasitoid species

Table 2 Parasitoid species emerged from the pupal chambers of *Cameraria ohridella* in Hungary in 1998

Parasitoid species	County		
	overwintering generation	1 st summer generation	2 nd summer generation
<i>Aprostocetus</i> sp.	Békés		Szabolcs-Szatmár-Bereg
<i>Baryscapus</i> sp.	Vas		
<i>Baryscapus nigroviolaceus</i>	Nógrád	Baranya	
<i>Chrysocharis pentheus</i>	Békés	Borsod-Abaúj-Zemplén	Győr-Moson-Sopron, Jász-Nagykun-Szolnok
<i>Chrysocharis</i> sp.		Békés	
<i>Cirrospilus</i> sp.			Budapest
<i>Cirrospilus vittatus</i>	Békés		
<i>Closterocerus trifasciatus</i>	Békés, Csongrád, Jász-Nagykun-Szolnok, Vas, Veszprém	Pest, Tolna	Csongrád, Hajdú-Bihar, Szabolcs-Szatmár-Bereg, Tolna
<i>Eupelmus vesicularis</i>	Csongrád		
<i>Macrocentrus</i> sp.		Pest	
<i>Minotetrastichus frontalis</i>	Békés, Budapest, Csongrád, Nógrád, Somogy, Jász-Nagykun-Szolnok, Veszprém	Baranya, Békés, Budapest, Heves, Pest, Somogy, Jász-Nagykun-Szolnok, Tolna, Vas	Békés, Borsod-Abaúj-Zemplén, Csongrád, Győr-Moson-Sopron, Hajdú-Bihar, Szabolcs-Szatmár-Bereg, Jász-Nagykun-Szolnok, Vas
<i>Pediobius saulius</i>	Baranya, Bács-Kiskun, Békés, Csongrád, Jász-Nagykun-Szolnok, Tolna	Baranya, Budapest, Békés, Csongrád, Nógrád, Jász-Nagykun-Szolnok, Tolna	Baranya, Bács-Kiskun, Csongrád, Hajdú-Bihar, Tolna
<i>Pediobius</i> sp.		Békés, Budapest, Csongrád, Jász-Nagykun-Szolnok, Nógrád, Tolna	
<i>Pnigalio pectinicornis</i>	Békés, Budapest, Somogy, Szabolcs-Szatmár-Bereg, Zala	Baranya, Budapest, Heves, Komárom-Esztergom, Nógrád, Somogy, Szabolcs-Szatmár-Bereg, Jász-Nagykun-Szolnok, Vas	Győr-Moson-Sopron, Komárom-Esztergom, Szabolcs-Szatmár-Bereg, Vas
<i>Pteromalus semotus</i>	Budapest, Komárom-Esztergom		
<i>Pteromalus</i> sp.		Jász-Nagykun-Szolnok	

were recovered. Out of the frequent species *Minotetrastichus frontalis*, *Pnigalio pectinicornis*, *Pediobius saulius* and *Closterocerus trifasciatus* were present in 14, 10, 9 and 5 counties. The most abundant species were *Minotetrastichus frontalis*, *Pnigalio pectinicornis* and *Pteromalus semotus*. The number of females were higher in the overwintering generation, while the number of males were higher in the summer generations (Tables 3 and 4).

Table 3 Parasitoid species emerged from the pupal chambers of *Cameraria ohridella* in Hungary in 1998

Parasitoid species	overwintering generation		1 st summer generation		2 nd summer generation	
	number of adults and species rate					
	No	%	No	%	No	%
<i>Aprostocetus</i> sp.	1	0,67	0	-	4	6,50
<i>Baryscapus</i> sp.	1	0,67	0	-	0	-
<i>Baryscapus nigroviolaceus</i>	1	0,67	1	0,99	0	-
<i>Chrysocharis pentheus</i>	1	0,67	1	0,99	2	3,20
<i>Chrysocharis</i> sp.	0	-	2	1,98	0	-
<i>Cirrospilus vittatus</i>	1	0,67	0	-	0	-
<i>Cirrospilus</i> sp.	0	-	0	-	2	3,20
<i>Closterocerus trifasciatus</i>	9	6,00	4	3,96	4	6,65
<i>Eupelmus vesicularis</i>	1	0,67	0	-	0	-
<i>Macrocentrus</i> sp.	0	-	1	0,99	0	-
<i>Minotetrastichus frontalis</i>	39	26,00	28	27,72	17	27,40
<i>Pediobius saulius</i>	10	6,67	0	-	22	35,50
<i>Pediobius</i> sp.	0	-	39	38,61	0	-
<i>Pnigalio pectinicornis</i>	82	54,67	24	23,76	10	16,10
<i>Pteromalus semotus</i>	4	2,67	0	-	0	-
<i>Pteromalus</i> sp.	0	-	1	0,99	0	-

Only 7 chalcidoid species were found in 1999-2000 (Table 5). The most frequent species were *Pediobius saulius*, *Minotetrastichus frontalis* and *Closterocerus trifasciatus*. Most of the species are primary parasitoids of lepidopteran species, viz. *Baryscapus nigroviolaceus*, *Chrysocharis pentheus*, *Cirrospilus vittatus*, *Closterocerus trifasciatus*, *Minotetrastichus frontalis* and *Pnigalio pectinicornis*, or rarely secondary parasitoids of their hymenopteran parasitoids on deciduous and herbaceous plants. *Pediobius saulius* and *Pteromalus semotus* are primary and often secondary parasitoids of lepidopteran and coleopteran species. The majority of parasitoid species is chalcidoid wasp from the families Eulophidae, Pteromalidae and Eupelmidae, but there are two braconid species among them viz. *Colastes flavitarsis*, and *Colastes vividus*.

The dominant parasitoids of closely related leaf miners occurring on fruit crops have found and accepted the pest of horse chestnut as host. *Minotetrastichus frontalis* was the most frequent species with quite dense population. *Pnigalio pectinicornis*, *Closterocerus trifasciatus* and *Pteromalus semotus* were the subdominant species. Level of parasitism showed a quite heterogeneous picture, depending on the locality and time of the study as well as on the generation of the host insect. Rearing results confirmed our hypothesis, set up when concluding our ecosystem studies. Data on level of parasitisation are quite variable, ranged between 0.0 and 43.2% during the three studied

years. We observed more or less parasitism on every area. Among the sampling sites, there were ones (Budapest, Margaret island) where, during two years parasitisation levels of both 0.0 and 32.5% were observed and we also found places (Budapest, Tövis street; Budapest, Castle district) where the recorded data were below 3.0%. Naturally we began to study the reasons of such differences. Knowing the place and surroundings of the infested trees, it was relatively easy to state that in the urban environment, poor in plant species, level of parasitisation was only from 0.0 to 5.5%, while in the ecologically diverse environment rich in species, data as high as from 20 to 40% were not scarce either.

Table 4 Sexual rate of parasitoid species emerged from the pupal chambers of *Cameraria ohridella* in Hungary in 1998 (Abbreviations: m – male, f – female)

Parasitoid species	overwintering generation				1 st summer generation				2 nd summer generation			
	m	f	total	m:f	m	f	total	m:f	m	f	total	m:f
<i>Aprostocetus</i> sp.	0	1	1		0	0	0		2	2	4	
<i>Baryscapus</i> sp.	0	1	1		0	0	0		0	0	0	
<i>Baryscapus nigroviolaceus</i>	0	1	1		0	1	1		0	0	0	
<i>Chrysocharis pentheus</i>	1	0	1		0	1	1		1	1	2	
<i>Chrysocharis</i> sp.	0	0	0		1	1	2		0	0	0	
<i>Cirrospilus vittatus</i>	1	0	1		0	0	0		0	0	0	
<i>Cirrospilus</i> sp.	0	0	0		0	0	0		0	2	2	
<i>Closterocerus trifasciatus</i>	3	6	9	1:2	1	3	4	1:0.3	1	3	4	1:0.3
<i>Eupelmus vesicularis</i>	1	0	1		0	0	0		0	0	0	
<i>Macrocentrus</i> sp.	0	0	0		1	0	1		0	0	0	
<i>Minotetrastichus frontalis</i>	9	30	39	1:3.3	11	17	28	1:1.5	8	9	17	1:1.1
<i>Pediobius saulius</i>	3	7	10	1:2.3					12	10	22	1:0.8
<i>Pediobius</i> sp.					25	14	39	1:0.6				
<i>Phigalia pectinicornis</i>	40	42	82	1:1.1	12	12	24	1:1	7	3	10	1:0.4
<i>Pteromalus semotus</i>	4	0	4		0	0	0		0	0	0	
<i>Pteromalus</i> sp.	0	0	0		1	0	1		0	0	0	

The establishment of a host-parasitoid relation on the horse chestnut trees in a castle park (at Nagykovácsi) with varied vegetation, surrounded by a forest, which means: in a situation characteristic of a diverse environment. Under undisturbed conditions, due to the lack of leaf miner control, in 1997 a considerable population of parasitoids could establish and reproduce, resulting in their effect on the third generation of the host species. Further the relatively favourable situation even improved by 1999, than we could detect parasitoids 43.2% of the specimens of the overwintering generation.

At Nagykovácsi such favourable situation was created, characterizing leaf miner – parasitoid relations in orchards where seasonal flight of the host insect occurred by 4-6 days earlier than that of the parasitoids. Such conditions allow treatments with insignificant side-effect on parasitoids until the beneficials will be able to maintain a balanced pest population.

In an environment poor in species, it was concluded from the studies of parasitism on the leaf miner population of horse chestnut trees grown in typical urban circumstances that though presence

of parasitoids could be detected, due to the very few species and low population density, they do not influence number of leaf miners.

Table 5 Parasitoid species emerged from the pupal chambers of *Cameraria ohridella* in Hungary in 1999-2000

Parasitoid species	County		
	overwintering generation	1 st summer generation	2 nd summer generation
<i>Chrysocharis pentheus</i>		Békés, Csongrád	
<i>Cirrospilus viticola</i>		Baranya, Pest	Bács-Kiskun
<i>Closterocerus trifasciatus</i>	Borsod-Abaúj-Zemplén, Komárom-Esztergom	Baranya, Bács-Kiskun, Békés, Heves, Jász-Nagykun-Szolnok, Szabolcs-Szatmár-Bereg, Tolna	Baranya, Bács-Kiskun, Békés, Csongrád, Heves, Pest, Somogy, Tolna, Vas, Veszprém
<i>Minotetrastichus frontalis</i>	Budapest, Komárom-Esztergom	Baranya, Bács-Kiskun, Békés, Borsod-Abaúj-Zemplén, Csongrád, Fejér, Komárom-Esztergom, Pest, Szabolcs-Szatmár-Bereg, Tolna, Vas, Veszprém	Baranya, Bács-Kiskun, Békés, Csongrád, Fejér, Komárom-Esztergom, Pest, Somogy, Vas, Veszprém
<i>Pediobius saulius</i>	Baranya, Borsod-Abaúj-Zemplén, Budapest, Komárom-Esztergom	Baranya, Bács-Kiskun, Békés, Borsod-Abaúj-Zemplén, Csongrád, Fejér, Hajdú-Bihar, Heves, Jász-Nagykun-Szolnok, Komárom-Esztergom, Nógrád, Somogy, Szabolcs-Szatmár-Bereg, Tolna, Vas, Veszprém, Zala	Baranya, Bács-Kiskun, Békés, Borsod-Abaúj-Zemplén, Csongrád, Fejér, Hajdú-Bihar, Heves, Komárom-Esztergom, Nógrád, Pest, Tolna, Vas, Veszprém
<i>Pnigalio pectinicornis</i>	Borsod-Abaúj-Zemplén		Nógrád, Szabolcs-Szatmár-Bereg
<i>Sympiesis gordius</i>		Pest	

Flight activities of summer generations of leaf miner populations and their parasitoids living on horse chestnut trees in a typical environment (evergreens, lawn, roses, asphalted roads and paved roads) were studied. Generally a single species belong to low population densities. Time of the flight and species of the parasitoids attacking horse chestnut leaf miner and emerging from it are almost completely incidental.

Conclusions

Studying the reason, it was concluded that intensity of establishment and richness in species of parasitoids mainly depend on the diversity of environment, while rate of increase and density of population are influenced by environmental conditions and human activity. The more diverse environment the horse chestnut has the more significant role of parasitoids in decreasing the pest population is.

It is worth considering treatments above parasitisation level of from 30 to 35%. If spraying is needed, it must be carried out observing not only the biology and flight activity of the leaf miner, but also that of the dominant parasitoids occurring on the place, in a way safe to parasitoids.

A parasitoid-friendly pest management programme, in addition to proper timing of application of IGR compounds, for example chitin synthesis inhibitors, involves giving up burning of the leaf litter in autumn. We concluded from our studies that the level of parasitisation is always the highest in the last, overwintering generation and burning kills not only the pest but its parasitoids, too.

Acknowledgements

We would like to thank Dr. Jenő Papp (Hungarian Natural History Museum, Budapest) for identifying braconid species. The authors wish to express their thanks to each entomologist of all the Plant Protection and Soil Conservation Services (formerly Plant Health and Soil Conservation Stations) viz. K. Avar, Margit Cziklin, Szilvia T. Gál, G. Gólya, Dr. Júlia Györffy Molnár, Dr. P. Gyulai, B. Havasréti, T. Hegyi, Dr. B. Herczig, P. Hertelendy, Dr. J. Jobbágy, I. Kasza, Dr. Mária J. Molnár, Klára Reider Saly, Piroska Szabó, Mária Szántó Veszélka, Dr. K. Szeőke, Gabriella L. Szendrey, B. Tóth, Éva Urfi Fogarasi, L. Vasas, Klára Várnai and G. Vörös, also to Krisztina Vásáros Mihályi, and Gyuláné Nyíri.

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ROLE OF NATURAL INSECT ENEMIES OF RICE GALL MIDGE, *ORSEOLIA ORYZAE* (WOOD–MASON) IN THAILAND

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Abstract – Study on the role of natural insect enemies of rice gall midge, *Orseolia oryzae* was carried out in Ubon Ratchathani province in non-chemical treated wet and dry season rice fields in 1994 and 1995. Three species of larval parasitoids, *Neanastatus cinctiventris*, *Neanastatus oryzae* and *Platygaster foersteri*, and one species of larval-pupal parasitoid, *Platygaster oryzae* were found during the wet season, with average 80.51% larval mortality caused by these parasitoids. Three species of larval parasitoids, *Obtusiclava oryzae*, *Neanastatus cinctiventris*, and *Neanastatus oryzae* and one species of larval-pupal parasitoid, *Platygaster oryzae* were found during the dry season, which from the two *Neanastatus* species and *Platygaster oryzae* were the most effective, caused 95.5% mortality of pest on the 7th week of observations.

Key words: *Orseolia oryzae*, Diptera, rice gall midge, parasitoids, Thailand

Introduction

Rice gall midge, *Orseolia oryzae* (Wood-Mason) (Diptera: Cecidomyiidae) is one of the most serious rice pests in Thailand. The gall midge causes high economically high damage every year. The female lays several hundred eggs and have 3-4 generations per year. Gray-white maggot-like larvae after hatching, move down on the leaf blade, between the leaf sheath and stem until they reach the growth point of apical or side buds at the node. The larva feed inside the developing bud, in the zone of new tillers differentiation, in a hollow chamber and induce gall formation around it. As the larva feeds, the tubular gall enlarges at the base, elongates and appears as an abnormal light green tiller. The pupa is light pink and becomes red before the emergence of the adult midge. The pupa has abdominal spines which it uses to brace itself while wiggling to the top of the gall in preparation for emergence as an adult, usually at night. The damage caused by the gall midge turns the rice tillers into tubular galls that do not bear panicles. Galls continue to grow after adults have emerged. A completely developed gall is a silvery – white hollow, which is called onion leaves or silver shoots.

Four important parasitoids of rice gall midge larvae and pupae had been found in Thailand: *Platygaster oryzae*, *Platygaster foersteri*, *Neanastatus gracillius*, and *Obtusiclava oryzae* (Doa 1983). Reissing *et al.* (1986) mentioned the next parasitoids of *Orseolia oryzae* larvae: *Platygaster oryzae*, *Neanastatus cinctiventris*, *Neanastatus oryzae*, and *Propicroscystus mirificus*.

There is many control measures for *O. oryzae* can be used: cultural control, using of resistant rice varieties, biological and chemical controls. Natural enemies are one of the most important factors for controlling *O. oryzae* populations, thus it is necessary to know their useful role and extend this knowledge to farmers for making decision for *O. oryzae* control strategy.

Materials and Methods

Randomly pick damage symptom of rice caused by *Orseolia oryzae* from each of 10 hills across the paddy. Hundred of silver shoots was collected from 0.16 acre per one replication, it have four replication fields. (Ubon Ratchathani) Record total number and damage number of *Orseolia oryzae* larva-pupa caused by natural enemies weekly. Identify kinds of natural enemies.

Results

Four species of parasitoids were found on *Orseolia oryzae* larvae in wet season: *Neanastatus cinctiventris* and *Neanastatus oryzae* (Chalcidoidea, Eupelmidae), *Platygaster foersteri* and *Platygaster oryzae* (Proctotrupoidea, Platigastridae), with average 81.51% infestation. Highest parasitization level for *N. cinctiventris* was observed on the 5th week – 22.3%; for *N. oryzae* on the 2nd week – 28.0%, for *P. foersteri* on the 2nd week also – 16.0%, and for *P. oryzae* on the 9th week – 70.0%.

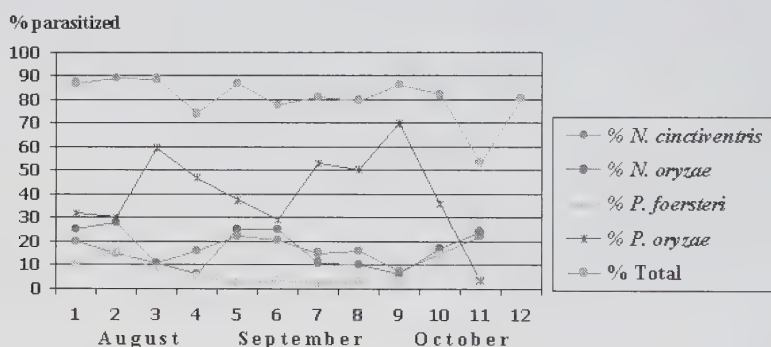


Figure 1 *Orseolia oryzae* larvae parasitization level in wet season rice field in Ubon Ratchathani province in 1994

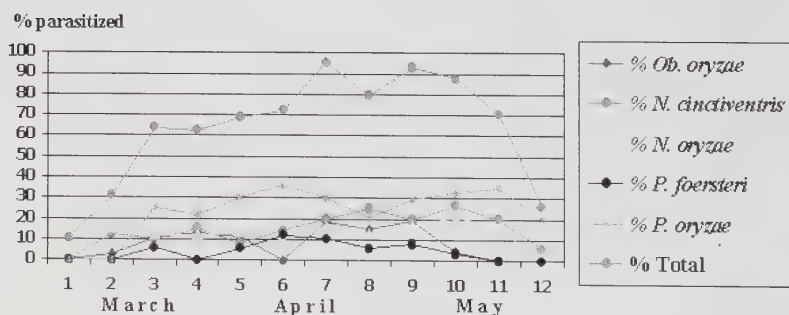


Figure 2 *Orseolia oryzae* larvae parasitization level in wet season rice field in Ubon Ratchathani province in 1994

Fivespecies of parasitoids were found on *Orseolia oryzae* larvae in dry season: *Obtusiclava oryzae*, *N. cinctiventris* and *N. oryzae*; *P. foersteri* and *P. oryzae*, with average 63.45% infestation. Highest parasitization level for *N. oryzae* was observedat on the 9th week – 16.55%, for *O. oryzae* on the 9th week – 19.0%, for *N. cintiventris* on the 10th week – 26.5%, for *P. foresteri* on the 6th week – 12.0%, and for *P. oryzae* on the 6th week also – 36.0%.

Conclusions

It was found that rice gall midge larvae and pupae were higher infested by parasitoids rather in wet season – average 81.51% than in dry season – average 63.45%.

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ROLE OF EGG PARASITIDS IN CONTROL OF RICE STEM BORER, *SCIRPOPHAGA INCERTULAS* (WALKER) POPULATIONS IN THAILAND

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Abstract – Studies on egg parasitoids of the rice stem borer – *Scirpophaga incertulas* (Walker) in wet season, non pesticide-treated rice fields from 6 provinces of Thailand: Chai Nat; Suphan Buri; Ratcha Buri; Nakhon Prathom; Prachin Buri & Phatthalung were carried out in 1994. Three species of egg parasitoids: *Telenomus rowani*, *Tetrastichus schoenobii*, and *Trichogramma japonicum* were found. The average rate of parasitization of 3 species was 59.0%. The highest one, 85.0% was found in Nakhon Prathom province, while the lowest was 40.0% in Phatthalung. The egg parasitoids can effectively control the pest, *S. incertulas*.

Key words: *Scirpophaga incertulas*, Lepidoptera, rice stem borer, parasitoids, Thailand

Introduction

Yellow rice stem borer, *Scirpophaga incertulas* (Walker) (Lepidoptera) is one of the major pests of rice in Thailand. Eggs are laid in oval batch near leaf tip. Newly hatched larvae with pale hairless yellow and small orange head often suspend themselves from leaves by a silken thread and are blown to other plants. Others make a tube from cut leaves, fall on the water and swim or drift to nearby plants. Young larvae feed on leaves and leaf sheaths. Medium-aged larvae penetrate the leaf sheath and feed between the sheath and tiller for several days before entering the stem. Older larvae feed inside the stem near the base of the plant. Mature larvae inside the stem may move below the soil surface and hibernate when the conditions are unfavorable. Damage caused by larvae during young stage of rice occurs at the central leaves of the damage tillers turn brown. This damage is called deadhearts. If damage occurs after spikelet, panicles turn white and no grain filling occurs. The damaged panicles are called whiteheads.

A Thai–German (1988–1993) warning project and report on pests forecasting showed that even the number of egg masses of *S. incertulas* is high, number of damaged deadhearts and whiteheads is still low what indicated the efficiency of egg parasitoids in control pest populations.

Napompeth (1982) reported the next parasitoid species reared from eggs of *S. incertulas*: *Tetrastichus schoenobii*, *Tetrastichus ayyari*, *Telenomus rowani*, *Telenomus dignus*, *Trichogramma japonicum*, *Trichogramma australicum*, and *Trichogramma chilotraeae*. Greathead (1979) mentioned that *Tetrastichus schoenobii* is the most effective egg parasitoid, parasitization of *S. incertulas* eggs can be as high as 70.0%.

Methods

Egg masses of *S. incertulas* were sampled and collected weekly and randomly across paddy field from rice seedlings from 50 days old till rice flowering stage of 90 days old. Hundred hills per each of 4 rice fields in each province were sampled (Table 1).



Results

Egg masses found in each field had from 1 to 48 eggs. The highest egg masses number was found in Suphan Buri where the average number of eggs was 9.75. The highest rate of egg parasitization was 5.75, found in Suphan Buri. Also in the Nakhon Prathom province from average 6.0 eggs per one laying, 5.5 was parasitized.

Three species of egg parasitoids were reared from eggs of *Scirpophaga incertulas*: *Telenomus rowani* (Gahan) (Proctotrupoidea: Scelionidae), *Tetrastichus schoenobii*, (Chalcidoidea: Eulophidae), and *Trichogramma japonicum* (Ashmead) (Chalcidoidea: Trichogrammatidae).

The surveillance officer teams reported that normally in non-chemical treated rice fields only seldom rice pests outbreaks were observed. In this study, 59% of *S. incertulas* eggs were infested by above-mentioned three species of egg parasitoids (Table).

So, we should encourage farmers to conserve natural enemies, particularly egg parasitoids and before using pesticide treatments they must estimate at first the possible impact of natural enemies onto pests' populations.

Table The total number of *Scirpophaga incertulas* egg masses in each rice field and the number of parasitized egg masses
(A – total number of egg masses; B – number of parasitized egg masses)

Pro-vince	Field No. I			Field No. II			Field No. III			Field No. IV			Average		
	A	B	%	A	B	%	A	B	%	A	B	%	A	B	%
Chai Nat	4	3	75	3	2	67	2	1	50	1	1	100	2.5	1.75	70
Suphan Buri	30	27	90	48	29	60	7	5	71	3	1	33	22	15.5	71
Ratcha Buri	10	4	40	11	10	91	7	1	14	11	8	73	9.75	5.75	59
Nakhon Prathom	10	9	90	11	11	100	2	1	50	1	1	100	6	5.5	92
Prachin Buri	7	2	29	11	8	72	5	3	60	1	0	0	6	3.25	54
Phattha Lung	5	2	40	7	3	43	6	2	33	9	4	44	6.75	2.75	41

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THE DIAMONDBACK MOTH, *PLUTELLA XYLOSTELLA* (L.) (LEPIDOPTERA: PLUTELLIDAE), AND ITS PARASITOIDS IN SOUTH AFRICA

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Abstract – In South Africa, diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is an important pest of cole crops but it is not as injurious as in other countries with similar climates. Larval and pupal populations of *P. xylostella* were monitored for a continuous period of five years in unsprayed cabbage fields near Brits, North-West Province, South Africa. Moth flights were monitored with synthetic sex pheromone traps. Samples of *P. xylostella* were taken into the laboratory and parasitoids that emerged were identified. Numbers of caught moths in the traps were low from January to July and much higher during August to December, peaking in spring during August to October. The moth flights corresponded with larval infestations in the crops. Larval infestations and crop damage were low from December to June but increased in spring and peaked at about 18–20 larvae per plant every year, between August and October. Parasitoids of *P. xylostella* were present throughout the year but with low incidence during the winter month (June – August). The fauna of *P. xylostella* parasitoids in the study area was found to be rich; during the study period 23 species of parasitoids and hyperparasitoids were identified. The most abundant parasitoids were the larval parasitoid *Cotesia plutellae* (Kurdjumov), the larval-pupal parasitoid *Oomyzus sokolowskii* (Kurdjumov), the pupal parasitoid *Diadromus collaris* Gravenhorst, and the hyperparasitoids *Mesochorus* sp. and *Pteromalus* sp. The rich fauna of *P. xylostella* parasitoids in South Africa indicates a very long association between parasitoids and the pest in the region.

Key words: *Plutella xylostella*, diamondback moth, biological control, parasitoid, South Africa

Introduction

Diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is the most injurious insect pest of cole crops throughout the world (Talekar & Shelton 1993). *Plutella xylostella* is the most universally distributed insect of all Lepidoptera (Meyrick 1928) and occurs wherever brassica crops are grown (Talekar & Shelton 1993). In many countries, *P. xylostella* has developed resistance to every synthetic insecticide used against it in the field (Talekar *et al.* 1990) including to toxins from the bacterium *Bacillus thuringiensis* (Tabashnik *et al.* 1990). Its control is estimated to cost about US\$ 1 billion annually (Talekar 1992). Lack of effective natural enemies is considered to be the major cause of the high pest status of *P. xylostella* in many parts of the world (Lim 1986). The destruction of natural enemies by the indiscriminate and widespread use of insecticides by farmers (Ooi & Sudderuddin 1978) is also considered to be the reason for the lack of effective natural control in most countries (Talekar & Shelton 1993).

In South Africa *P. xylostella* is an important pest of cole crops (Annecke & Moran 1982) but it is not as injurious as in other countries with similar climates (Kfir 1996). The biology of *P. xylostella* was first studied in South Africa by Gunn (1917) and its natural enemies by Ulyett



(1947). In more recent studies Kfir (1997, 1998) studied the parasitoids of *P. xylostella* in South Africa and concluded on the basis of the abundance of parasitoids and indigenous plants from the Brassicaceae that *P. xylostella* might have evolved in southern Africa and not in the Mediterranean region of Europe as is widely accepted by entomologists (Hardy 1938; Harcourt 1954).

This is an updated report on previous work (Kfir 1997, 1998) on the parasitoids of *P. xylostella* with additional information on moth flights and seasonal occurrence of larvae and pupae of the pest in cabbage crops in South Africa.

Materials and Methods

Larvae, pupae and moths populations of *P. xylostella* were monitored for a continuous period of five years (from March 1993 to February 1998) in cabbage, *Brassica oleracea* var. *capitata*, fields at Hartebeespoort Agricultural Research Station near Brits (25°38'S, 27°47'E; altitude 1102m), North-West Province, South Africa. Cabbage is cultivated throughout the year in the region and in most parts of southern Africa since heat-tolerant cultivars have been developed (Hemy 1984). As three cabbage crops were planted each year, a total of 15 consecutive crops have been monitored.

Standard cultivation methods as practised in the region, including weeding, fertilising and irrigation were used but no chemical pest control measures were applied. At weekly intervals, for the duration of the study, 30 plants were selected randomly and scouted for larvae and pupae of *P. xylostella* and its parasitoids cocoons. Samples of eggs, larvae, pupae and parasitoid cocoons were collected and taken to the laboratory. In the laboratory, the pupae and the parasitoid cocoons were transferred individually into glass vials (2.5 x 10 cm). Larvae were provided with sections of fresh cabbage leaves and kept individually in Petri dishes. Cabbage leaves were provided every second day until the larvae pupated or parasitoid cocoons formed. Eggs were kept in glass vials until they hatch. Insects were held in the laboratory at $22 \pm 2^\circ\text{C}$, $60 \pm 5\%$ RH, and pupation of larvae and emergence of moths and parasitoids were recorded. Emerged parasitoids were identified.

Three delta-shaped Synthetic sex-pheromone traps were deployed in each crop in order to monitor flights of *P. xylostella* male moth populations. In the traps, sticky floors coated with a layer of polybutene adhesive were used. The sticky floors were replaced weekly when the traps were examined and moth catches recorded. The pheromone dispensers were placed in the middle of the sticky floor within the metal trap (26 X 9.5 X 13 cm high). Pheromone dispensers (provided by AgriSense-BCS Limited, UK) were replaced every 6 weeks.

Voucher specimens of parasitoids have been deposited in the National Collection of Insects, Biosystematics Division, Plant Protection Research Institute, Pretoria.

Results and Discussion

Trap catches of male moths indicated that in the study area *P. xylostella* was on the wing throughout the year. Numbers of caught moths were low from January to July and much higher during August to December, peaking in spring during August to October (Fig. 1). Although the flight pattern was similar throughout the study period, its intensity differed from year to year. The lowest flight intensity was recorded during 1993-1994 study period when moth catches peaked at

24 moths per trap per week in mid-October 1993 and on average for the whole study period each trap caught a total of 212 moths. On the other hand, during 1994-1995 study period moth catches peaked at 99 moths during the second part of September 1994 and a total of 948 moths were caught (Fig. 1).

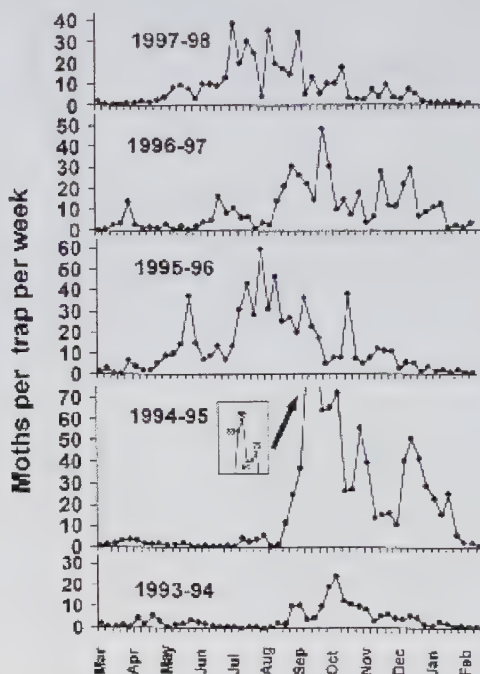


Figure 1 Five consecutive years of synthetic sex-pheromone trap catches of *Plutella xylostella* male moths at Brits, North-West Province, South Africa

The moth flights corresponded with larval infestations in the crops. Larval infestations and crop damage were relatively low from December to June when infestation levels fluctuated between zero and five larvae/plant. Larval and pupal infestations increased in spring and peaked at about 18–20 larvae/plant every year, between August and October (Fig. 2). In 1994-95 study period infestation was exceptionally high when a peak population of 75 larvae/plant were recorded during second part of September (Fig. 2).

Parasitoids of *P. xylostella* were present throughout the year but with low incidence during the winter month (June–August) when very few parasitoids emerged from the field-collected samples. During the study 23 species of parasitoids and hyperparasitoids were identified.

No egg parasitoids were recorded in this study. Two egg-larval parasitoids were recorded; *Chelonus curvimaculatus* Cameron and *Chelonus* sp. (Hymenoptera: Braconidae). Eggs of *P. xylostella* were attacked by females of the two *Chelonus* species and after the parasitoid larvae completed development it emerged from the fully-grown caterpillar hosts to spin its own cocoon. *Chelonus curvimaculatus* is a polyphagous parasitoid able to parasitise and develop in several other lepidopteran hosts (Kfir 1995; Broodryk 1969).

The most abundant larval parasitoid was the solitary endoparasitoid *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae). This parasitoid has been introduced into several countries for biological control of *P. xylostella* (Lim 1986, 1992; Fitton & Walker 1992). Other larval parasitoids were *Apanteles halfordi* Ulyett (Hymenoptera: Braconidae), *Cotesia* sp., *Habrobracon brevicornis* (Wesmael) (Hymenoptera: Braconidae) and *Peribaea* sp. (Diptera: Tachinidae). *Apanteles halfordi* was active during spring and summer. Recent taxonomic studies suggest that *A. halfordi* is a senior synonym of *Apanteles eriophyes* Nixon, a matter that will be dealt with in the taxonomic literature (G.L. Prinsloo, *pers. comm.*). This species is specific to *P. xylostella* and is known only from South Africa (Walker & Fitton 1992). Taylor (1932) reported the biology of *H. brevicornis* in South Africa. It occurs in Afrotropical, Nearctic, Neotropical, Oriental and Palaearctic Regions (Van den Berg *et al.* 1988).

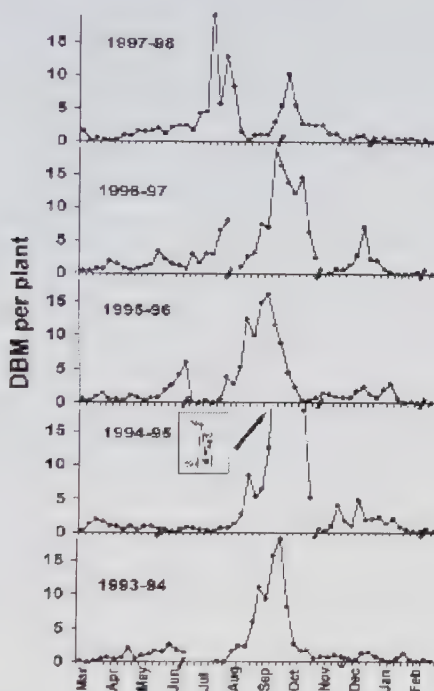


Figure 2 Abundance (infestations by larvae and pupae per plant per week) of *Plutella xylostella* during a five year period in unsprayed cabbage (three cabbage crops per year) at Brits, North-West Province, South Africa

Three larval-pupal parasitoids were recorded. The most abundant was *Oomyzus sokolowskii* (Kurdjumov) (Hymenoptera: Eulophidae), which is the only gregarious primary parasitoid of *P. xylostella*. Up to 20 individuals may complete development in one host but normally only about 8-10 individuals emerge. It occurs in Europe, Asia and Africa (Harcourt 1960) and its biology was described by Ooi (1988) and Mushtaque (1990). *Oomyzus sokolowskii* has been introduced into several countries for biological control of *P. xylostella* (Lim 1992; Cock 1983). In this study

O. sokolowskii occasionally acted also as a hyperparasite and emerged from cocoons of *C. plutellae*. The other larval-pupal parasitoids were *Diadegma mollipla* (Holmgren) (Hymenoptera: Ichneumonidae) and *Itopectis* sp. (Hymenoptera: Ichneumonidae). Recently, Azidah *et al.* (2000) taxonomically revised the species of *Diadegma* attacking *P. xylostella* and reported that *D. mollipla* is an Afrotropical species occurring also on some Indian and South Atlantic islands. It is also a parasitoid of the potato tuber moth, *Phthorimaea operculella* (Zeller). Broodryk (1971) studied its biology in South Africa.

The most abundant pupal parasitoid was *Diadromus collaris* Gravenhorst (Hymenoptera: Ichneumonidae). It was very common during the autumn months (April and May) and spring months (August and September). *Diadromus collaris* has been introduced into New Zealand (Hardi 1938), Australia (Wilson 1960) and Malaysia (Ooi & Lim 1989) for biological control of *P. xylostella*. Other pupal parasitoids were *Brachymeria* sp. and *Hockeria* sp. (Hymenoptera: Chalcididae), *Tetrastichus howardi* (Olliff) (Hymenoptera: Eulophidae) and an unidentified ichneumonid. *Tetrastichus howardi* is an introduced species in South Africa (Kfir *et al.* 1993). It was recorded from *P. xylostella* in Malaysia (Talekar & Shelton 1993) and is widely distribution through Pakistan, Mauritius and eastern Australia (Bouček 1988).

Hyperparasitoids were active in spring (September to October) when *P. xylostella* populations were high and primary parasitoids abundant. During the remaining of the year they were rare. The most abundant hyperparasitoids were *Mesochorus* sp. (Hymenoptera: Ichneumonidae) and *Pteromalus* sp. (Hymenoptera: Pteromalidae). Both emerged from cocoons of their primary parasitoid hosts. *Mesochorus* sp. attacked *P. xylostella* larvae previously parasitised by *C. plutellae* or *A. halfordi*, but killed the primary parasitoids only after they had formed cocoons. *Pteromalus* sp. directly attacked cocoons of *C. plutellae*, *A. eriophyes*, *D. mollipla* and occasionally *D. collaris*. Other hyperparasitoids were *Aphanogmus fijiensis* (Ferrière) (Hymenoptera: Ceraphronidae), *Eurytoma* sp. (Hymenoptera: Eurytomidae), *Tetrastichus* sp. (Hymenoptera: Eulophidae), *Hockeria* sp., *Brachymeria* sp. and *Proconura* sp. (Hymenoptera: Chalcididae). All these hyperparasitoids are solitary except *A. fijiensis*. Between 4 to 7 *A. fijiensis* emerged from each cocoon of *C. plutellae* or *A. halfordi*.

The fauna of DBM parasitoids in South Africa was found to be rich. The 23 species of parasitoids and hyperparasitoids reared from *P. xylostella* larvae and pupae in South Africa indicate a very long association between parasitoids and the pest in the region.

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EGG PARASITIDS OF *PERIPLANETA AMERICANA* IN CHIANG MAI, THAILAND

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Abstract — Six species of cockroaches in two families were collected in 22 districts of Chiang Mai Province of Thailand and domination of each species was estimated: four species in the family Blattidae, *Neostylopyga rhombifolia* (54.9%), *Periplaneta americana* (19.2%), *P. brunnea* (11.7%), and *P. australasiae* (8.96%); and two species in the family Blaberidae, namely, *Pycnoscelus surinamensis* (4.99%) and *Nauphoeta cinerea* (0.18%). Two egg parasitoids, *Evania appendigaster* (Evanoidea: Evanidae) and *Tetrastichus hagenowii* (Chalcidoidea: Eulophidae) were reared from *N. rhombifolia* and *P. americana*. The total level of parasitization in both cockroach species was only 1.0%, which from 60.0% was caused by *T. hagenowii* in *P. americana* eggs. Parasitization levels of *P. americana* ootheca laid at the corner of ceiling, on the wall and on the floor by *Tetrastichus hagenowii* were 5.26%, 7.89%, and 2.63% respectively.

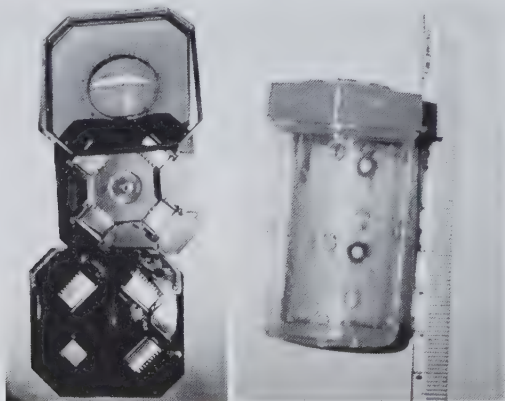
Key words: Blattidae, *Periplaneta americana*, parasitoids, Thailand

Introductions

From 25 cockroach species known in Thailand, only 9 of them are found in households (Sujumong 1982). According to a cockroach survey done in 5 provinces of North-Eastern part of Thailand (Khon Kaen, Nong Kai, Maha Sarakam, Nakorn Ratchasima, and Ubol Ratchathani) by Jeungwiwattanaporn (1984); nine species of cockroaches from three families were found: three species in the family Blattelidae – *Supella longipalpa* (Fab.), *Blatella germinica* (L.), and *B. lituricollis* (Walker); 4 species in the family Blattidae – *Neostylopyga rhombifolia* (Stoll), *Periplaneta australasiae* (Fab.), *P. americana* (L.), and *P. brunnea* (Burmeister); and two species from Blaberidae – *Pycnoscelus indicus* (Fab.) and *Nauphoeta cinerea* (Oliver). Above 24 species of Hymenoptera parasitoids from 6 families are known to parasitize several species of cockroach (Cameron 1955). Cockroaches are not only sources of nuisance by destroying materials such as papers and releasing foul odour around their habitats, but also disease transmitters.

Materials and Methods

Chiang Mai province, with a total area of 20,107 km² which from 83% is mountainous, locates in the northern part of Thailand, at an altitude of 310 m a.s.l. Cockroaches were collected from ten houses in a village that was randomly chosen from preselected subdistrict in each district of Chiang Mai province. The average time spent in hand catching process was about 25 minutes per house, following by overnight trapping with cockroach trap. Collection of parasitoids for american cockroach, *P. americana* was also carried out at the same time. An oothecae aged 2–5 days old was stuck on a small cardboard and placed in a small plastic bottle of 3 cm in diameter and 5 cm high, with holes around the bottle for parasitoids' penetrating (Figs 1-2). Each bottle was adhered near the locations where cockroaches were common during the 25-day collections.



Figures 1–2 Cockroach traps

Two sets of experiments with *Tetrastichus hagenowii* (Chalcidoidea: Eulophidae) – egg parasitoid in oothecae of *P. americana* were performed in a student campus room (4.8 x 6.8 x 3.8 m). The room was screened for existing ootheca and egg's parasitoids before starting each experiment. Two oothecae aged 25 days, were attached to each corner of the room at ceiling, wall, and floor. Parasitoids were released from parasitized ootheca at the middle of the floor to start the experiment. Each experiment was carried out for 10 days before recollection of ootheca for examination of parasitization rate. 240 female and 44 male parasitoids came out from oothecae in the first experiment and 120 females and 22 males in the second one.

Results and Discussions

Six cockroach species from two families were found in households of 22 districts in Chiang Mai province: four species from the family Blattidae – *Neostylopyga rhombifolia* (54.9%), *Periplaneta americana* (19.2%), *P. brunnea* (11.7%), and *P. australasiae* (8.96%); two species from the family Blaberidae – *Pycnoscelus surinamensis* (4.99%) and *Nauphoeta cinerea* (0.18%). Although Jeungwiwatnaporn (1984) had reported three cockroach species from the family Blattellidae from North-Eastern part of Thailand, none of these species were found in this survey. None of the surveyed district had all six cockroach species. Chai Pra Kan is the district with the highest cockroach species number (15.3%) while only 0.65% of them were found in Mae Wang district. There was no correlation between occupation of the home owner, house characteristics, floor type, and items found in the household such as books and clothes, and number of six cockroach species, except for *Periplaneta brunnea* which for significant (0.05) correlation between number of books and population density was showed.

Two egg parasitoids, *Evania appendigaster* (Evanoidea: Evanidae) and *Tetrastichus hagenowii* (Chalcidoidea: Eulophidae) were reared from oothecae of *Neostylopyga rhombifolia* and *Periplaneta americana*. Parasitoids were found only in 5 districts (Muang, San Sai, San Kam Pang, San Pa Tong, and Chiang Dao). The total level of parasitization of both parasitoids on both cockroach species was only 1.0% which from 60.0% due to *T. hagenowii* parasitization on *P. americana*.

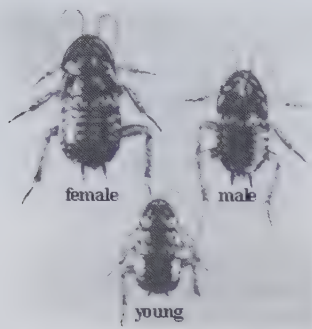


Figure 3 *Neostylopyga rhombifolia* (Stoll)

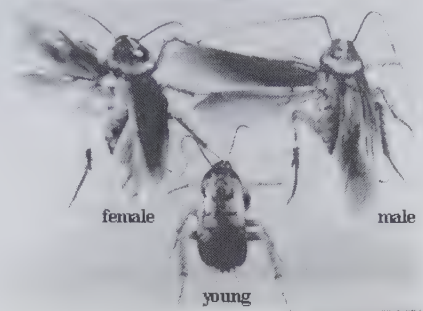


Figure 4 *Periplaneta americana* (L.)

Table 1 Percentage of cockroach species in households from each district in Chiang Mai province

District	<i>Neostylopyga rhombifolia</i>	<i>Periplaneta brunnea</i>	<i>Periplaneta americana</i>	<i>Periplaneta australasiae</i>	<i>Pycnoscelus surinamensis</i>	<i>Nauphoeta cinerea</i>	Subtotal
Chai Pra Kan	3.51	11.08	0.00	0.74	0.00	0.00	15.33
Hang Dong	6.37	0.74	3.60	2.59	0.83	0.00	14.13
Hod	6.65	0.19	0.28	0.00	0.00	0.00	7.12
Sarapee	6.00	0.55	0.18	0.00	0.00	0.00	6.73
Fang	2.49	1.02	0.00	2.77	0.09	0.00	6.37
Doi Sa Ket	2.49	1.48	0.37	0.19	1.20	0.00	5.73
Jom Tong	3.42	0.74	1.01	0.00	0.19	0.00	5.36
San Kam Pang	3.88	0.37	0.74	0.00	0.19	0.00	5.18
Prao	3.05	0.28	0.55	0.46	0.00	0.00	4.34
Mae Rim	2.13	1.20	0.00	0.18	0.65	0.18	4.34
Om Koi	3.42	0.09	0.37	0.00	0.09	0.00	3.97
Mae Jam	1.94	0.09	1.48	0.00	0.00	0.00	3.51
Muang	1.57	0.83	0.00	0.28	0.00	0.00	2.68
Viang Hang	0.92	0.00	0.74	0.37	0.46	0.00	2.49
Mae Tang	0.46	0.00	1.85	0.18	0.00	0.00	2.49
Doi Tao	1.38	0.09	0.37	0.00	0.00	0.00	1.84
Mae Eye	0.74	0.37	0.00	0.37	0.28	0.00	1.76
Sa Meung	1.48	0.00	0.00	0.00	0.18	0.00	1.66
San Sai	0.55	0.09	0.18	0.74	0.09	0.00	1.65
San Pa Tong	0.83	0.00	0.00	0.00	0.74	0.00	1.57
Chiang Dao	1.01	0.00	0.00	0.09	0.00	0.00	1.10
Mae Wang	0.65	0.00	0.00	0.00	0.00	0.00	0.65
Subtotal	54.94	19.21	11.72	8.96	4.99	0.18	100.00

The parasitization level in both experiments was similar, despite differences of parasitoid density used in the two experiments: 2 and 1 females per m³ respectively. Roth & Willis (1954) also performed a similar experiment with *T. hagenowii* population of 1000 individuals released onto 96 oothecae of *P. americana* in a room size 4.8 x 5.1 x 3.9 m³ without tenant. The parasitization ratio used by Roth & Willis (1954) was 8.0 ootheca per 100 parasitoids in comparison to 1.8 oothecae in this experiment.

Table 2 Parasitization efficiency of *T. hagenowii* on *P. americana*

Location of ootheca	Parasitized ootheca (%)	# of parasitoid offspring	
		Females	Males
Experiment 1:	240 females and 44 males		
Ceiling corner	0.00	0	0
Wall corner	10.53	107	8
Floor corner	5.26	61	5
Subtotal	15.79	168	13
Experiment 2:	120 females and 22 males		
Ceiling corner	10.53	113	21
Wall corner	5.26	60	5
Floor corner	0.00	0	0
Subtotal	15.79	173	26

Conclusions

Six cockroach species were found in 22 districts of Chiang Mai province: *N. rhombifolia* (54.9%), *P. americana* (19.2%), *P. brunnea* (11.7%), *P. australasiae* (8.96%), *P. surinamensis* (4.99%), and *N. cinerea* (0.18%). Chai Pra Kan is the district with the highest cockroach population of 15.3% while only 0.65% of them were found in Mae Wang district. There was a significant statistical relationship between the number of books and population of *Periplaneta brunnea*. Two cockroach species, namely; *N. rhombifolia* and *P. americana* were found to attack by twoegg parasitoids, *Evania appendigaster* and *Tetrastichus hagenowii*. Parasitization level of *T. hagenowii* on oothecae of *P. americana*, placed at the corner of the ceiling, wall and the floor was found to be 16.0% in a student campus room with two tenants.

The reason of low parasitizing efficiency in nature might be caused by uneven distribution of parasitoids in the area and the season selected for the collection of oothecae. In this survey, the collection of oothecae was carried out between the end of rainy season and throughout the cold season, at which time the cockroach populations are low.

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THE PARASITOID AND HYPERPARASITOID COMPLEX CONTROLLING *PLUTELLA XYLOSTELLA* (L.) (LEPIDOPTERA: PLUTELLIDAE) POPULATIONS IN MOLDAVIA-ROMANIA

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Abstract – The complex of parasitoids and hyperparasitoids associated with diamondback moth (*Plutella xylostella* (L.)), a destructive pest of cabbage in Romania, is given. Over 25 species of primary and secondary parasitoids are identified. The dynamics of these species over time, from one crop to another and from one area to another are discussed. Species, which play an important role in the biological control of this pest, and those, which could be used in biocontrol are also discussed.

Key words: *Plutella xylostella*, cabbage, parasitoid, hyperparasitoid, biological control

Introduction

Plutella xylostella (L.) (Lepidoptera: Plutellidae) is one of the dangerous pests attacking cabbage crops. The most dangerous attack affects small plants, when they are transferred from hotbeds to the fields, because larvae destroy the buds on which they live. In Moldavia the species have three generations in the southern region and two in the north.

A complex of parasitoids controls *Plutella xylostella* populations. The parasitization level sometimes is 50-90% and even 100%.

Materials and Methods

Field works were carried out in 13 locations during 1999-2000. *Plutella xylostella* larvae and pupae were collected with further laboratory rearing for estimating role of parasitoids in controlling this pest. From 889 collected adult larvae and pupae, 167 died during the laboratory rearing because of various factors: bacteria, viruses, etc., and from the rest 722 individuals (58.75%) parasitoids emerged.

Results and Discussions

In different studied locations, the parasitization rate varies from 0 up to 100%. In six sites the parasitization level was up to 100%, whereas in other six it was less than 70% (Table).

Table Synecological analysis of the primary parasitoids in the populations of *Plutella xylostella* (L.)

No.	Species	Abundance	Dominance	Constancy	Index of ecological significance			
1.	<i>Diadegma armillata</i>	238	32.9	D ₅	100	C ₄	32.9	W ₅
2.	<i>Diadegma chrysosticta</i>	112	15.5	D ₅	100	C ₄	15.5	W ₅
3.	<i>Diadegma fenestralis</i>	88	12.1	D ₄	78	C ₃	9.4	W ₄
4.	<i>Diadegma holopyga</i>	41	5.6	D ₄	72	C ₃	4.0	W ₄
5.	<i>Thyraeella collaris</i>	39	5.4	D ₄	66	C ₃	3.5	W ₄
6.	<i>Diadromus subtilicornis</i>	36	5.0	D ₃	66	C ₃	3.3	W ₄
7.	<i>Diadegma tenuipes</i>	31	4.2	D ₃	60	C ₃	2.5	W ₄
8.	<i>Diadegma trochanterata</i>	21	2.9	D ₃	48	C ₂	1.3	W ₃
9.	<i>Apanteles plutellae</i>	19	2.6	D ₃	48	C ₂	1.2	W ₃
10.	<i>Diadegma semiclausum</i>	17	2.3	D ₃	30	C ₂	0.6	W ₂
11.	<i>Apanteles rubecula</i>	16	2.2	D ₃	30	C ₂	0.6	W ₂
12.	<i>Apanteles ruficrus</i>	14	1.9	D ₂	24	C ₁	0.4	W ₂
13.	<i>Diadegma vestigialis</i>	11	1.5	D ₂	24	C ₁	0.3	W ₂
14.	<i>Hyposoter ebeninus</i>	13	1.1	D ₂	18	C ₁	0.1	W ₁
15.	<i>Itopectis alternans</i>	6	0.8	D ₁	18	C ₁	0.1	W ₁
16.	<i>Diadegma germanica</i>	5	0.6	D ₁	12	C ₁	0.07	W ₁
17.	<i>Diadegma hygrobia</i>	5	0.6	D ₁	12	C ₁	0.07	W ₁
18.	<i>Diadegma crassa</i>	5	0.4	D ₁	12	C ₁	0.002	W ₁
19.	<i>Diadegma interrupta</i>	1	0.1	D ₁	6	C ₁	0.002	W ₁
TOTAL		722						

Nineteen species of primary parasitoids and 9 species of secondary parasitoids were reared:

Primary parasitoids:

Ichneumonidae: 1. *Diadegma armillata* Grav., 2. *D. chrysosticta* Gmel., 3. *Diadegma fenestralis* Holmgr., 4. *Diadegma holopyga* Thoms., 5. *Diadegma hygrobia* Thoms., 6. *Diadromus subtilicornis* Grav., 7. *Diadegma tenuipes* Thoms., 8. *Diadegma trochanterata* Thoms., 9. *Diadegma semiclausum* Helln., 10. *Diadegma vestigialis* Ratz., 11. *Hyposoter ebeninus* Grav., 12. *Diadegma interrupta* Holmgr., 13., 14. *Diadegma crassa* Bridgm., 15. *Diadegma germanica* Horstm., 16. *Itopectis alternans* Grav., *Thyraeella collaris* Grav.

Braconidae: 1. *Apanteles plutellae* Mues., 2. *Apanteles ruficrus* (Hal.), 3. *Apanteles rubecula* Marsh.

Secondary parasitoids:

Ichneumonidae: 1. *Mesochorus anomalus* Holmgr., hyperparasitoid of *Apanteles ruficrus* (Hal.) and *A. rubecula* Marsh.; 2. *Mesochorus orbitalis*, hyperparasitoid of *Apanteles rubecula* Marsh. and *A. plutellae* Mues. 3. *Mesochorus facialis* hyperparasitoid of *Apanteles ruficrus* (Hal.) and *A. plutellae* Mues.; 4. *Lysibia varitarsus* Grav., hyperparasitoid of *Apanteles plutellae* Mues.; 5. *Mesochorus vittator* Zett., hyperparasitoid of *Diadegma fenestralis* Holmgr., *D. armillata* Grav. and *D. chrysosticta* Gmel.

Pteromalidae: 1. *Dibrachys cavus* (Walk.) hyperparasitoid of *Diadegma fenestralis* Holmgr. and *D. chrysosticta* Gmel.; 2. *Eupteromalus* sp., hyperparasitoid of *D. armillata* Grav., *D. chrysosticta* Gmel. and *D. trochanterata* Thoms.

Eulophidae: 1. *Tetrastichus* sp. hyperparasitoid of *Apanteles plutellae* Mues.

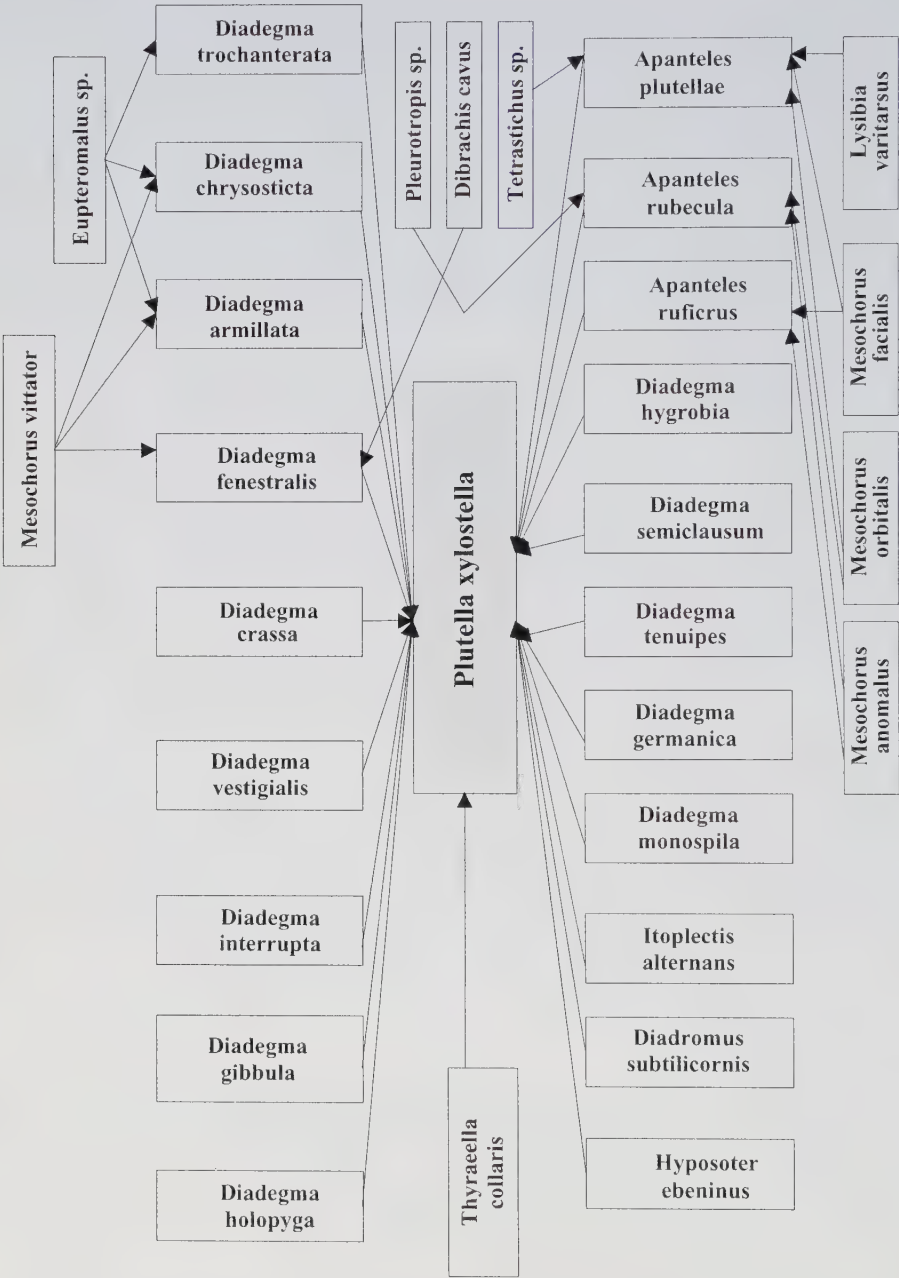


Figure 1 Parasitoid complex of *Plutella xylostella* (L.)



Conclusions

From 889 collected final instar larvae and pupae of *Plutella xylostella*, 722 individuals (58.75%) were parasitized.

For the first time, *Diadegma tenuipes* Thoms. and *Diadegma crassa* Bridgm. are mentioned as parasitoids of *P. xylostella*. Also trophical relationships of hyperparasitoids, *Mesochorus anomalus* Holmgr. and *Mesochorus orbitalis* Holmgr. with *Apanteles* species are given for the first time.

The tri-trophic relationship “*Plutella xylostella*-primary parasitoids-hyperparasitoids” is also showed. A synecological analysis with estimated parasitoid's abundance, constancy, dominance and index of ecological significance is given.

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BIOLOGICAL CONTROL OF PLANTHOPPER, *METCALFA PRUINOSA* SAY BY *NEODRYINUS TYPHLOCYBAE* ASHMEAD

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Abstract – The predator and parasitoidal effect of the wasp (*Neodryinus typhlocybae* Ashmead) on planthopper (*Metcalfa pruinosa* Say) has been studied on three ornamental bush species: *Acer pseudoplatanus* L., *Cornus sanguinea* L. and *Ligustrum vulgare* L. The trial was performed in special insectaria near Nova Gorica during 1999. On *Ligustrum vulgare* 42 larvae of plant hopper were killed by the wasp, on *Cornus sanguinea* 57 larvae were killed and on *Acer pseudoplatanus* 71 larvae were killed. The wasps on *A. pseudoplatanus* had a lifetime of 28 days compared to 25 days of those on *Cornus sanguinea* and 24 days on *Ligustrum vulgare*.

Key words: Biological control, *Metcalfa pruinosa*, *Neodryinus typhlocybae*, *Acer pseudoplatanus*, *Cornus sanguinea*, *Ligustrum vulgare*

Introduction

In the last decades new plant pests spread to Slovenia either by themselves or by man (Milevoj 1998). Among others also the planthopper (*Metcalfa pruinosa* Say) was detected, American species from Flatidae family. In the year 1979 it was first found in Italy, in the Treviso region (Zangheri & Donadini 1980), and later in Slovenia (Šivic 1991). It was recorded in France during 1985, in Switzerland as well as in Croatia during 1993.

The planthopper is a polyphago, feeding on over 170 species of cultivated or wild growing plants from 60 families (Duso & Pavan 1987; Seljak 1993). Cicada sucks out sap from the plants, excretes a lot of honeydew which together with smuttiness prevents photosynthesis, and makes plants dirty. Chemical control is not successful enough, because the pests can immigrate to the previously sprinkled plants. In the natural environment there is not enough of natural enemies to control it.

Like in Italy (Girolami & Camporese 1994; Girolami *et al.* 1999; Girolami & Mazzon 1999) also in Slovenia the possibility of a classical biological control of this organism was researched by importing the monophagous predator parasitic wasp *Neodryinus typhlocybae* Ashmead (Hymenoptera: Dryinidae), an effective natural enemy in its native country (America) (Girolami & Camporese 1994).

Materials and Methods

The field experiment was performed in an isolated location in the Nova Gorica neighbourhood. The preferential host plants for the planthopper were: *Cornus sanguinea* L., *Ligustrum vulgare* L. and *Acer pseudoplatanus* L. In simple insectaria the predator parasitic relations among cicadas and



wasps were being observed. The insectaria were fixed to the branches of the host plants. The experiment was performed with the both organisms and one control in four repetitions for each plant. Predatory activity of wasps feeding on planthoppers was studied, their eaten larvae were counted, parasitoid activity of wasps was controlled by ovipositions in L₃, L₄ and L₅ phase. The lifetime of wasp was controlled too.

Results and Discussion

The experiment on wasp cultivating on planthoppers on some chosen host plants was succesful. The wasp survived in researched natural conditions in Slovenia. The Table 1 shows the predatory and parasitic potential of the wasps (*Neodryinus typhlocybae* Ashmead). Average efficiency of *Neodryinus typhlocybae* at controlling *Metcalfa pruinosa* was 42 killed planthopper larvae and laying of eggs in its larvae on *Ligustrum vulgare* L., 57 on *Cornus sanguinea* L. and 71 on *Acer pseudoplatanus*. The life expectancy of wasps was the longest (28 days) on *Acer pseudo-*
platanus L., on *Cornus sanguinea* lasted 25 days, and on *Ligustrum vulgare* 24 days.

Table 1 Predatory and parasitoid activity of *Neodryinus typhlocybae* Ashmead

Host plants	Repetition/ Average	Number of plant- hopper larvae (L ₁ , L ₂) consumed by <i>N. typhlocybae</i> (a)	Number of wasp eggs laid into L ₃ , L ₄ , L ₅ of <i>M. pruinosa</i> (b)	Σ (a + b)	Life time of wasp (in days)
<i>Cornus sanguinea</i>	1	31	14		25
	2	34	27		27
	3	26	7		18
	4	44	45		29
		34	23	57	25
<i>Acer pseudoplatanus</i>	1	31	14		23
	2	42	38		29
	3	39	36		29
	4	44	41		31
		39	32	71	28
<i>Ligustrum vulgare</i>	1	28	15		27
	2	26	8		23
	3	29	18		23
	4	29	16		23
		28	14	42	24

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SPECIES COMPOSITION OF PARASITIDS (HYMENOPTERA) ON APPLE FEEDING PHYLLONORYCTER (LEPIDOPTERA: GRACILLARIIDAE) IN BULGARIA

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Abstract – Parasitoid complexes of leafminers, *Phyllonorycter blancardella* (Fabricius), *P. corylifoliella* (Hübner) and *P. pyrifoliella* (Gerasimow) in unsprayed apple orchards in Bulgaria were studied. Forty five parasitoid species were found. Thirty seven of them belong to the family Eulophidae, one to Encyrtidae, six to Braconidae and one to Ichneumonidae. Comparison of parasitoid complex of the three leafminer species from different regions is presented. Forty parasitoid species were isolated from *P. blancardella*. The most abundant were *Cirrospilus staryi* Boucek, *Sympiesis sericeicornis* Nees, *Achrysocharoides cilla* Walker and *Apanteles arisba* Nixon. The parasitic wasps *Achrysocharoides zwölferi* Delucchi, *A. altilis* Delucchi and *A. niveipes* Thomson were the most abundant among the twenty-two species, isolated from *P. corylifoliella*. The leafminer *P. pyrifoliella* was parasitized by twelve parasitoids. The most important were *Sympiesis sericeicornis* Nees and *Holcothorax testaceipes* (Ratzeburg). *H. testaceipes* was isolated from *P. blancardella* too, but it was quite rare. The parasitoids from fam. Braconidae *Apanteles circumscriptus* (Nees) and *A. arisba* Nixon were important regulators of population density of *Phyllonorycter* species on apples in Bulgaria too.

Key words: leafminer, *Phyllonorycter*, parasitoid, apple, Bulgaria

Introduction

Apple orchards in Bulgaria are infested by three leafminer species from genus *Phyllonorycter* Hbn. (Lepidoptera: Gracillariidae). They are *Phyllonorycter blancardella* (Fabricius), *P. corylifoliella* (Hübner) and *P. pyrifoliella* (Gerasimow).

There are many studies concerning parasitoid complex of the spotted tentiform leafminer *P. blancardella* (Pottinger & LeRoux, 1971; Dimic 1984; Casas & Baumgärtner 1990; etc.) Research by Van Driesche and Taub (1983); Ridgway & Mahr (1985); Maier (1990) and others has shown that parasites do have excellent potential to regulate leafminer populations on unsprayed plants. There are some data concerning the parasitoids of *P. corylifoliella* but in literature there is little information about natural enemies of *P. pyrifoliella* (Vereshchagina *et al.* 1968; Ivanov & Slavov 1986).

First data concerning the parasitoids of *P. blancardella* and *P. corylifoliella* in Bulgaria were presented by Ivanov & Slavov (1975). According to Ivanov (1976), Slavov (1980), and others important species for control of *P. blancardella* and *P. corylifoliella* were *Sympiesis sericeicornis* and *Apanteles circumscriptus*. All their investigations were made in region of Plovdiv and on sprayed orchards. In addition they did not make separation of parasitoids of the two moth species. Studies on parasitoid complexes of *Phyllonorycter* spp in Bulgaria were made by Pelov *et al.* (1993) and 43 species were isolated. Pelov & Tomov (1998) presented a list of parasitoids reared from leafminers on fruit trees in Bulgaria.

During the last 10 years there were great changes in economic and agriculture of Bulgaria. The large apple orchards were separated and destroyed. That fact gave me a unique opportunity to study the species diversity of parasitoids on apple feeding *Phyllonorycter* in unsprayed for 10 years orchards of Bulgaria.

Materials and Methods

The study was conducted during the period 1997-1999. Mined leaves with overwintering generation of *P. blancardella*, *P. corylifoliella* and *P. pyrifoliella* were gathered in autumn from unsprayed apple trees (*Malus* spp.) from six fruit growing regions of Bulgaria with different climate – Sofia, Kyustendil, Petrich, Plovdiv, Silistra and Staro Oryahovo.

Samples of 200 mined leaves were kept outdoors for overwintering. In next spring mines to be reared out were placed in glass tubes. The samples were held at 18–20°C in laboratory to induce parasitoid emergence. The emerged parasitoids were calculated.

Results

As a result of the study forty-five parasitoid species were isolated from apple feeding *Phyllonorycter*. The species diversity of parasitoids was the richest in *P. blancardella* (forty species). Twenty-two species were isolated from *P. corylifoliella* and 12 from *P. pyrifoliella* (Table 1). The proportion of parasitoids isolated from *P. blancardella* is presented in Table 2. Parasitoid species were not observed to differ in the three plots during the two years of investigations. It concerned the relative abundance of the species too. The situation was the same in parasitoid complex of *P. corylifoliella* (Table 3) and *P. pyrifoliella* (Table 4).

The most abundant species in complex of *P. blancardella* were *C. staryi*, *S. sericeicornis*, *A. cilla* and *A. arisba*. The abundance of the four species was 80% of all parasitoids found. The parasitic wasps *A. zwöelferi*, *A. altilis* and *A. niveipes* were the most abundant among the species, isolated from *P. corylifoliella*. The relative abundance of the three species was about 60%. The completely different was the situation with parasitoid complex of *P. pyrifoliella*. During the period of study the complex was strongly dominated by *H. testaceipes* about 80% followed by *S. sericeicornis*, *S. gordius* etc.

Discussion

The absence of insecticide treatment of studied apple orchards during the last 10 years led to restoration of the rich diversity of parasitic wasps playing role as regulators of population density of leafminers on apples. The isolated species were twice more than species observed by the other authors. The results showed increasing role of *Achrysocharoides* species in parasitoid complex of apple feeding *Phyllonorycter* in Bulgaria in comparison with results of Slavov (1980). It seems that they prefer the upper-site mines made by *P. corylifoliella*. Interesting fact is the domination of *Holcorthorax testaceipes* only in parasitoid complex of *P. pyrifoliella*. The investigation of Tomov & Pelov (1998) showed different proportion of the three moth species in studied regions of Bulgaria. It was found that there were regions where *P. blancardella* was absent. Such regions



Table 1 List of parasitoids reared from *Phyllonorycter blancardella* (F.), *P. corylifoliella* (Hb.) and *P. pyrifoliella* (Grsm.) in Bulgaria

Parasitoid species	<i>P. blancardella</i>	<i>P. corylifoliella</i>	<i>P. pyrifoliella</i>
1. <i>Achrysocharella formosa</i> Westwood	+	+	-
2. <i>Achrysocharoides altilis</i> Delucchi	+	+	-
3. <i>Achrysocharoides atys</i> Walker	+	+	-
4. <i>Achrysocharoides cilla</i> Walker	+	-	-
5. <i>Achrysocharoides insignitellae</i> Erdős	-	-	+
6. <i>Achrysocharoides latreillei</i> Curtis	+	+	+
7. <i>Achrysocharoides niveipes</i> Thomson	+	+	-
8. <i>Achrysocharoides splendens</i> Delucchi	-	+	-
9. <i>Achrysocharoides zwoelferi</i> Delucchi	-	+	-
10. <i>Chrysocharis albiscapus</i> Erdős	+	-	-
11. <i>Chrysocharis idyia</i> Walker	+	+	-
12. <i>Chrysocharis laomedon</i> Walker	+	-	-
13. <i>Chrysocharis nephereus</i> Walker	+	-	-
14. <i>Chrysocharis orchestis</i> Ratzeburg	+	+	+
15. <i>Chrysocharis pentheus</i> Walker	+	+	-
16. <i>Cirrospilus diallus</i> Walker	+	-	-
17. <i>Cirrospilus elegantissimus</i> Westw.	+	-	-
18. <i>Cirrospilus lyncus</i> Walker	+	-	-
19. <i>Cirrospilus pictus</i> Nees	+	-	-
20. <i>Cirrospilus staryi</i> Bouček	+	+	+
21. <i>Cirrospilus variegatus</i> Masi	-	+	-
22. <i>Elachertus artaeus</i> Walker	+	-	-
23. <i>Elachertus inunctus</i> Nees	+	-	-
24. <i>Euterastichus amethystinus</i> Ratzeburg	+	+	-
25. <i>Minotetrastichus frontalis</i> Walker	+	+	-
26. <i>Pediobius pyrgo</i> Walker	+	-	-
27. <i>Pediobius saulius</i> Walker	+	-	-
28. <i>Pnigalio longulus</i> Zetterstedt	+	-	+
29. <i>Pnigalio pectinicornis</i> Linnaeus	+	+	+
30. <i>Pnigalio soemius</i> Walker	+	-	-
31. <i>Pnigalio xerophilus</i> Erdős	+	-	-
32. <i>Sympiesis acalle</i> Walker	+	+	-
33. <i>Sympiesis albiscapus</i> Erdős	+	-	-
34. <i>Sympiesis euspilapterygis</i> Erdős	+	-	+
35. <i>Sympiesis gordius</i> Walker	+	+	+
36. <i>Sympiesis sericeicornis</i> Nees	+	+	+
37. <i>Sympiesis viridula</i> Thomson	+	-	-
38. <i>Holcothorax testaceipes</i> Ratzeburg	+	-	+
39. <i>Colastes braconius</i> Haliday	+	-	+
40. <i>Apanteles arisba</i> Nixon	+	+	-
41. <i>Apanteles bicolor</i> (Nees)	+	+	-
42. <i>Apanteles circumscriptus</i> (Nees)	+	+	-
43. <i>Apanteles laetus</i> Marshall	+	+	-
44. <i>Apanteles phaetusa</i> Nixon	+		
45. <i>Scambus annulatus</i> (Kiss)			+

Table 2 The proportion of parasitoids isolated from *Phyllonorycter blancardella* (F.) in Bulgaria. Plot A – Sofia, Plot B – Kyustendil, Plot C – Plovdiv (%)

Parasitoid species	1997-1998			1998-1999		
	A	B	C	A	B	C
1. <i>A. formosa</i>	2.1	1.2	1.1	1.3	1.1	1.2
2. <i>A. altilis</i>	-	1.5	1.6	2.1	1.9	1.8
3. <i>A. atys</i>	1.5	2.6	1.4	2.0	2.2	1.5
4. <i>A. cilla</i>	15.0	14.5	14.3	14.8	14.9	15.2
5. <i>A. latreillei</i>	2.5	3.0	1.5	1.5	1.6	0.6
6. <i>A. niveipes</i>	-	0.4	0.2	0.1	-	2.0
7. <i>Ch. albiscapus</i>	0.1	0.1	0.2	0.1	0.1	-
8. <i>Ch. idyia</i>	0.1	0.1	0.1	-	0.1	0.1
9. <i>Ch. laomedon</i>	-	0.2	0.3	0.1	-	0.2
10. <i>Ch. nephereus</i>	1.1	-	0.1	1.1	1.0	0.1
11. <i>Ch. orchestis</i>	2.1	-	0.1	0.1	-	0.2
12. <i>Ch. pentheus</i>	1.0	0.1	0.3	0.8	0.2	1.0
13. <i>C. diallus</i>	0.1	-	0.1	0.1	-	0.1
14. <i>C. elegantissimus</i>	-	0.1	-	-	0.1	-
15. <i>C. lyncus</i>	0.1	0.2	0.2	0.1	0.2	0.1
16. <i>C. pictus</i>	3.8	3.2	0.1	1	0.9	-
17. <i>C. staryi</i>	32.0	29.0	28.9	31.0	32.0	30.5
18. <i>E. artaeus</i>	-	0.1	-	-	-	0.1
19. <i>E. inunctus</i>	-	0.1	-	0.1	0.1	0.1
20. <i>E. amethystinus</i>	-	0.2	0.3	0.5	-	0.2
21. <i>M. frontalis</i>	1.0	3.0	1.1	1.5	2.1	0.9
22. <i>P. pyrgo</i>	-	0.1	0.1	0.1	0.1	-
23. <i>P. saulius</i>	0.3	0.1	0.1	0.2	0.1	0.1
24. <i>P. longulus</i>	0.5	0.1	-	0.1	-	0.1
25. <i>P. pectinicornis</i>	3	5.5	3.8	3.2	3.0	3.9
26. <i>P. soemius</i>	0.5	0.4	0.4	0.1	0.2	0.1
27. <i>P. xerophilus</i>	-	0.1	-	-	0.1	-
28. <i>S. acalle</i>	0.3	0.1	0.1	-	0.2	0.1
29. <i>S. albiscapus</i>	0.1	0.2	-	-	0.1	-
30. <i>S. euspilapterygis</i>	0.3	-	-	0.1	-	-
31. <i>S. gordius</i>	-	0.1	0.1	0.2	-	-
32. <i>S. sericeicornis</i>	20.0	22.3	21.0	24.0	22.5	26.2
33. <i>S. viridula</i>	0.1	-	0.1	0.1	0.2	-
34. <i>H. testaceipes</i>	-	0.1	0.1	-	0.1	0.1
35. <i>C. braconius</i>	0.1	-	0.1	-	1.1	-
36. <i>A. arisba</i>	7.5	8.2	8.0	7.9	8.0	6.4
37. <i>A. bicolor</i>	-	-	0.1	1.9	0.5	-
38. <i>A. circumscriptus</i>	4.3	4.0	4.9	3.6	3.5	4.0
39. <i>A. laetus</i>	0.1	-	0.1	0.1	0.6	0.1
40. <i>A. phaetusa</i>	0.2	0.1	0.1	0.1	1.2	-

Table 3 The proportion of parasitoids reared from *Phyllonorycter corylifoliella* (Hb.) in Bulgaria. Plot A – Sofia, Plot B – Kyustendil, Plot C – Plovdiv (%)

Parasitoid species	1997-1998			1998-1999		
	A	B	C	A	B	C
1. <i>A. formosa</i>	1.2	4.9	4.3	4.9	4.0	3.9
2. <i>A. altilis</i>	22.1	23.0	21.6	22.3	22.0	21.5
3. <i>A. atys</i>	3.8	-	3.9	3.0	3.3	3.8
4. <i>A. latreillei</i>	4.2	3.3	3.0	3.6	1.8	3.6
5. <i>A. niveipes</i>	10.9	9.2	10.6	11.0	10.5	10.2
6. <i>A. splendens</i>	4.2	4.0	-	3.9	-	3.2
7. <i>A. zwoelferi</i>	30.0	29.0	32.0	33.0	33.3	34.6
8. <i>Ch. idyia</i>	-	1.1	1.1	0.1	2.1	-
9. <i>Ch. orchestis</i>	1.2	1.2	3.3	1.3	1.2	0.9
10. <i>Ch. pentheus</i>	2.3	2.4	3.0	1.2	1.3	1.9
11. <i>C. staryi</i>	2.1	0.1	1.2	0.6	1.2	0.1
12. <i>C. variegatus</i>	0.1	0.3	0.4	0.2	0.3	0.1
13. <i>E. amethystinus</i>	-	1.1	0.1	0.1	-	0.1
14. <i>M. frontalis</i>	2.5	2.3	1.5	2.6	2.4	2.6
15. <i>P. pectinicornis</i>	6.5	3.6	4.2	4.5	4.1	3.8
16. <i>S. acalle</i>	0.1	-	0.1	0.1	0.1	0.1
17. <i>S. gordius</i>	0.1	0.1	0.1	0.1	2.1	0.1
18. <i>S. sericeicornis</i>	5.1	5.2	2.9	4.8	3.0	4.0
19. <i>A. arisba</i>	1.0	2.5	0.2	-	2.1	0.1
20. <i>A. bicolor</i>	0.4	-	2.1	0.1	0.2	2.2
21. <i>A. circumscriptus</i>	2.1	4.6	4.4	2.5	5.0	3.1
22. <i>A. laetus</i>	0.1	2.1	-	0.1	-	0.1

Table 4 The proportion of parasitoids reared from *Phyllonorycter pyrifoliella* (Grsm.) in Bulgaria. Plot A – Silistra, Plot B – Staro Oryahovo, Plot C – Petrich (%)
(* only one crop, 5 January to 8 March 1999)

Parasitoid species	1997-1998			1998-1999		
	A	B	C	A	B	C
1. <i>A. insignitellae</i>	0.1	0.1	-	1.1	1.2	-
2. <i>A. latreillei</i>	0.1	0.1	0.3	0.8	1.2	1.2
3. <i>Ch. orchestis</i>	3.0	2.0	2.6	3.2	2.5	3.9
4. <i>C. staryi</i>	0.1	-	0.1	-	0.2	-
5. <i>P. longulus</i>	0.2	0.1	-	0.2	-	-
6. <i>P. pectinicornis</i>	1.1	0.2	2.6	2.1	3.2	2.0
7. <i>S. euspilapterygis</i>	0.1	0.1	0.2	0.1	-	0.2
8. <i>S. gordius</i>	6.0	4.0	5.2	5.2	3.6	3.4
9. <i>S. sericeicornis</i>	8.0	7.2	6.8	7.0	5.0	6.0
10. <i>H. testaceipes</i>	81.0	86.0	82.0	80.0	82.0	83.0
11. <i>C. braconius</i>	0.1	0.1	0.1	0.2	1.1	0.1
12. <i>S. annulatus</i>	0.2	0.1	0.1	0.1	-	0.2

were in Northeast part of Bulgaria where the apple orchards were infested mainly by *P. pyrifoliella* and single specimens of *P. corylifoliella*. On the other hand *P. pyrifoliella* was absent in the other part of Bulgaria except of Southwest region (Petrich) where the infestation on apples were by mixed population of *P. pyrifoliella* and *P. blancardella*. *H. testaceipes* was isolated from *P. blancardella* too, but it was quite rare.

Apanteles circumscriptus and *A. arisba* (Braconidae) were important regulators of population density of *Phyllonorycter* species on apples in Bulgaria too.

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TAXONOMIC ANALYSIS AND ECOLOGICAL PECULIARITIES OF HYMENOPTERAN PARASITIDS OF LEAF-MINERS IN APPLE ORCHARDS IN UKRAINE

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Abstracts – Seventy two hymenopterous parasitoid species were reared from larvae and pupae of leaf miners on apple trees in Ukraine. Twenty three species (32%) belong to Ichneumonoidea and 49 (68%) to Chalcidoidea. The biology, ecological peculiarities and host-parasitoid relationships were investigated.

Key words: leaf miners, apple orchard, parasitoid, Ukraine

Introduction

Twenty six species of leaf-miners from Lepidoptera, Diptera and Coleoptera are trophically associated with apple-trees in Ukraine (Zerova *et al.* 1992). The most common and harmful are the next lepidopterous species: *Nepticula malella* Stt. (Nepticulidae), *Leucoptera scitella* Z. (Lyonetiidae), *Phyllonorycter pyrifoliella* Grsm., *P. corylifoliella* Haw., *P. blancardella* F. (Gracillariidae); occasionally *Rhamphus oxyecantae* Marsh. (Coleoptera: Curculionidae), *Phythomyza heringiana* Hend (Diptera: Agromyzidae). Entomophagous insects play an important role in the regulation of these apple pests. In non-treated orchards infestation of mines by parasitoids can be as high as 70.0-90.0% (Balázs 1984; Balázs *et al.* 1984; Ivanov & Slavov 1986; Zerova *et al.* 1992 and others).

Results and Discussion

Parasitoid complexes of leaf-miner Lepidoptera, Coleoptera and Diptera on apple trees in different regions of Ukraine were studied. As the result 72 hymenopterous parasitoid species were reared from larvae and pupae of leaf miners, which from 23 species (32%) belong to Ichneumonoidea and 49 (68%) to Chalcidoidea. Their biology, host-parasitoid relationships were investigated. Species composition, peculiarities of biology and host-parasitoid relationships are given in the Table 1.

The most important group of parasitoids in the regulation of leaf-miners' populations is the Chalcidoidea, first of all Eulophidae, which are represented in this complex by 44 species. The most common and widespread eulophid species are: *Sympiesis sericeicornis*, *S. gordius*, *Cirrospilus vittatus*, *Chrysocharis pentheus*, *C. nitetis*, and others. Also a polyembryonic encyrtid wasp, *Holcothorax testaceipes* Ratz. is economically very important. Two braconid wasps, *Apanteles bicolor* and *A. circumscriptus* are also very important in this complex.

Table 1 Parasitoids of lepidopteran apple leaf-miners and some life-history peculiarities (I – primary, II – secondary, III – tertiary parasitoids; S – solitary, G – gregarious, Pm – polyembrionic; EN – endo-, EC – ectoparasitoid; O-L – egg-larval, L – larval, N – prepupal, L-P – larval-pupal, L/P – larval and pupal, P – pupal parasitoid)

#	Parasitoid species	Level of parasitism	Peculiarities of the life history (host interaction)
ICHNEUMONIDAE			
1.	<i>Itoplectis alternans</i> (Gravenhorst)	I-II	S, EN, P
2.	<i>Scambus annulatus</i> (Kiss)	I-II	S, EC, L
3.	<i>Scambus calobatus</i> (Gravenhorst)	I-II	S, EC, L
4.	<i>Scambus detritus</i> (Holmgren)	I	S, EC, L
5.	<i>Gelis areator</i> (Panzer)	II	S, EC, L
6.	<i>Mesochorus</i> sp.	II	S, EN, L
7.	<i>Herpestomus nasutus</i> Wesmael	I	S, EN, P
BRACONIDAE			
8.	<i>Colastes braconius</i> Haliday	I	S, EC, L
9.	<i>Oncophanes minutus</i> Wesmael	I	G (S), EC, L
10.	<i>Rysipolis hariolator</i> Haliday	I	S, EC(?), L
11.	<i>Gnaptodon georginae</i> Achterberg	I	S, EN, L
12.	<i>Gnaptodon pumilio</i> Nees	I	S, EN, L
13.	<i>Adelius erythronotus</i> Foerster	I	S, EN, L
14.	<i>Adelius subfasciatus</i> Haliday	I	S, EN, L
15.	<i>Apanteles ater</i> Ratzeburg	I	G (S), EN, L
16.	<i>Apanteles corvinus</i> Reinhard	I	S, EN, L
17.	<i>Apanteles xanthostigma</i> Haliday	I	S, EN, L
18.	<i>Dolichogenidia longicauda</i> (Wesmael)	I	S, EN, L
19.	<i>Pholetesor arisha</i> (Nixon)	I	S, EN, L
20.	<i>Pholetesor bicolor</i> (Nees)	I	S, EN, L
21.	<i>Pholetesor circumscriptus</i> (Nees)	I	S, EN, L
22.	<i>Pholetesor elpis</i> (Nixon)	I	S, EN, L
23.	<i>Mirax rufilabris</i> Haliday	I	S, EN, L
EUPELMIDAE			
24.	<i>Eupelmus urozonus</i> Dalman	I-II	G (S), EN, L
PTEROMALIDAE			
25.	<i>Dibrachys cavus</i> (Walker)	I-II-III	G, EC, L/P
26.	<i>Pteromalus dispar</i> (Curtis)	I-II	S/G, EN, L/P
27.	<i>Pteromalus semotus</i> (Walker)	I-II	S/G, EN, L/P
EULOPHIDAE			
28.	<i>Colpoclypeus florus</i> (Walker)	I	G, EC, L
29.	<i>Diglyphus isaea</i> (Walker)	I	S/G, EC, L
30.	<i>Pnigalio agraulis</i> (Walker)	I-II	S, EC, L
31.	<i>Pnigalio longulus</i> (Zetterstedt)	I	S, EC, L
32.	<i>Pnigalio pectinicornis</i> (Linnaeus)	I-II	S, EC, L
33.	<i>Pnigalio soemius</i> (Walker)	I	S, EC, L
34.	<i>Sympiesis acalle</i> (Walker)	I-II	S, EC, L
35.	<i>Sympiesis gordius</i> (Walker)	I-II	S, EC, L/P

#	Parasitoid species	Level of parasitism	Peculiarities of the life history (host interaction)
36.	<i>Sympiesis ringoniella</i> (Kamijo)	I	S, EC, L
37.	<i>Sympiesis sericeicornis</i> (Nees)	I-II	S, EC, L/P
38.	<i>Cirrospilus lyncus</i> Walker	I-II	S, EC, L
39.	<i>Cirrospilus talizkii</i> Bouček	I	S, EC, L
40.	<i>Cirrospilus viticola</i> (Rondani)	I-II	G/S, EC, L/P
41.	<i>Elachertus lateralis</i> (Spinola)	I	G, EC, L
42.	<i>Elachertus inunctus</i> Nees	I	G, EC, L
43.	<i>Elachertus isadas</i> (Walker)	I	G, EC, L
44.	<i>Achrysoharoides latreillei</i> (Curtis)	I	G/S, EN, L
45.	<i>Achrysoharoides niveipes</i> (Thomson)	I	G/S, EN, L
46.	<i>Achrysoharoides zwölferi</i> (Delucchi)	I	S, EN, L
47.	<i>Chrysocharis entedonoides</i> (Walker)	I	S, EN, L/P
48.	<i>Chrysocharis nephereus</i> (Walker)	I	S/G(?), EN, L
49.	<i>Chrysocharis nitetis</i> (Walker)	I-II	S, EN, L/P
50.	<i>Chrysocharis pentheus</i> (Walker)	I-II	S, EN, L
51.	<i>Chrysocharis phryne</i> (Walker)	I	S, EN, L-P
52.	<i>Chrysocharis prodice</i> (Walker)	I	S, EN, L
53.	<i>Chrysocharis pubens</i> (Delucchi)	I	S, EN, L/P
54.	<i>Chrysocharis pubicornis</i> (Zetterstedt)	I	S, EN, L-P
55.	<i>Closterocerus formosa</i> (Westwood)	I-II	S/G, EN, L
56.	<i>Closterocerus lanassa</i> (Walker)	I	S, EN, L
57.	<i>Closterocerus lyonetiae</i> (Ferrière)	I	S, EN, L
58.	<i>Closterocerus trifasciatus</i> Westwood	I-II	S/G, EN, L
59.	<i>Entedon punctiscapus</i> Thomson	I	S, EN, L
60.	<i>Pediobius metallicus</i> (Nees)	I-II	S, EN, L/P
61.	<i>Pediobius alcaeus</i> (Walker)	I-II	S, EN, L/P
62.	<i>Pediobius cassidae</i> Erdős	I-II	S/G, EN, L/P
63.	<i>Pediobius pyrgo</i> (Walker)	I-II	S/G, EN, L/P
64.	<i>Pediobius saulius</i> (Walker)	I-II-III	G, EN, L/P
65.	<i>Pediobius tetratomus</i> (Thomson)	II	S/G, EN, L
66.	<i>Pediobius bruchicida</i> (Rondani)	I-II	G, EN, L/P
67.	<i>Baryscapus galactopus</i> (Ratzeburg)	I-II	G, EN, L/P
68.	<i>Baryscapus nigroviolaceus</i> (Nees)	I-II-III	G/S, EN, L/P
69.	<i>Minotetrastichus frontalis</i> (Nees)	I-II-III	G/S, EC, L/P
70.	<i>Minotetrastichus platanellus</i> (Mercet)	I-II	G/S, EC, L/P
71.	<i>Tetrastichus miser</i> (Nees)	I	S, EC, L
ENCYRTIDAE			
72.	<i>Holcothorax testaceipes</i> (Ratzeburg)	I	Pm, EN, L

Majority of species in this complex – 48 – are primary parasitoids. Number of species (28) develop as primary-secondary parasitoids, e.g. *Sympiesis*, *Pnigalio*, *Cirrospilus*, *Pediobius*. Majority of species are oligophagous or polyphagous. Narrow oligophagous are represented with a few species only, e.g. *Apanteles bicolor*, *A. arisba*, some species of the genus *Gnaptodon*, also *Holcothorax testaceipes*.

Some ichneumonid species are not included into the table, however, they are represented in this complex, however, are very rare on leaf-miners.

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INDIGENOUS PARASITOIDS FOR THE CONTROL OF *MARUCA VITRATA* F. (LEPIDOPTERA: PYRALIDAE) IN THE PHILIPPINES

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Abstract – The bean podborer, *Maruca vitrata* F. is a major constraint to production of yardlong beans in the Philippines. Resistance to insecticides by *M. vitrata* has been reported in several countries, consequently research has focused more on biological control. This study was conducted under Philippine lowland conditions to identify indigenous parasitoids for control of *M. vitrata*. We identified one egg parasitoid, *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae), and three larval-pupal parasitoids, *Exorista xanthaspis* (Diptera: Tachinidae), *Peribaea orbata* (Diptera: Tachinidae), and *Bassus asper* (Hymenoptera: Braconidae). *B. asper* was the most prevalent species observed with parasitism rates up to 17.1% in unsprayed *V. sesquipedalis* fields. Parasitism rate in insecticide treated fields was less than in untreated. We tested in laboratory bioassays the effect of the common synthetic insecticides chlorpyrifos, deltamethrin, methomyl, and carbaryl to *B. asper* adults. Mortality was observed after 48 hours and the LC₅₀-values calculated using probit analysis. *B. asper* was highly susceptible to all insecticides. The data presented shows, that *B. asper* can contribute to the control of *M. vitrata* on *V. sesquipedalis* if insecticides are not used.

Key words: *Bassus asper*, *Maruca vitrata*, biological control, Southeast Asia

Introduction

The bean podborer *Maruca vitrata* F. (Lepidoptera: Pyralidae) is a major pest on leguminous crops in many tropical countries (Sharma 1998; Machuka *et al.* 1999). Yield reductions of 20-60% have been reported due to this pest (Singh & Van Emden 1979). In the Philippines *M. vitrata* was in 2001 found to be resistant against the commonly used synthetic insecticides chlorpyrifos, deltamethrin, methomyl, and carbaryl (Ulrichs *et al.* 2001a). Farmers respond to increasing pest problems with higher doses of insecticides.

Because of the economic importance of *M. vitrata* and the fact, that chemical control is difficult, we were evaluating the possibility of biological control approaches. Barrion *et al.* (1997) lists a total of 17 species of indigenous parasites for *M. vitrata* in the Philippines. Sison *et al.* (1996) reported up to 40% parasitism of *M. vitrata* larvae by an unknown wasp in Central Luzon. For any biological control program to be implemented, a thorough search for and accurate identification of existing natural enemies and potential biological control agents must be made. The aim of this study was to determine parasitoid species, which can be used for biological control of *M. vitrata* in the Philippines. We analyzed the impact of rainfall and insecticide application on the efficacy of parasitoid species.

Materials and Methods

The study was carried out at the Central Luzon State University (CLSU) in the Philippines. CLSU is located on the main-island of the Philippines Luzon, 150 km in the north of Metro Manila. We collected *M. vitrata* larvae from infested yardlong beans, *Vigna sesquipedalis*, at the experimental area of CLSU and on farm fields in San Leonardo (34 km south of CLSU) and San Jose (14 km north of CLSU). Yardlong beans were grown according to recommended agronomic practices (Aganon *et al.* 1997). We assume that farmer fields have been treated with insecticides. Farmers usually apply insecticide cocktails, with two or three active ingredients together. Yardlong bean plants on CLSU campus were unsprayed, except some experimental plots were treated with chlorpyrifos (200 g a.i. ha⁻¹).

Climate

Field experiments were conducted under tropical lowland conditions. Data was collected by the Philippine Atmospheric Geophysical Astronomical Service Administration on CLSU campus.

Egg parasitism

Eggs of the bean podborer were difficult to detect in the field, because they are small and translucent. To facilitate identification of egg parasites we wrapped leaf petioles of cowpea, *Vigna unguiculata*, in wet cotton and placed them into a rearing chamber to 15 *M. vitrata* pairs. Eggs laid on leaves were counted under a microscope and placed in insecticide free *V. sesquipedalis* fields. After 24 h they were returned into the laboratory and reared until larvae or parasites hatch.

Larval and pupal parasitism

Each week over five cropping periods from 1998 to 2000 we collected *M. vitrata* larvae in *V. sesquipedalis* fields. Larvae were reared individually in 100 ml plastic containers on artificial diet until parasitoids or adults hatched. Percent parasitism of pupae was determined by counting only parasitoids hatched from field collections of 5th instar larvae that became pupae within 48 hours after collection.

Artificial diet

The basic diet consists of 150 ml tap water, to which are added, 40 g of yardlong bean seed powder, 5 g potato-dextrose agar, and 14 g of a commercial diet for *Spodoptera* ssp. from Bioserve, Inc, City, State USA. The solution is blended and 1 g of a vitamin suspension added. The vitamin suspension contains a vitamin B complex, vitamin K, C, and niacin, and was obtained from the National Crop Protection Center in Los Banos, Philippines. The diet was autoclaved at 121 °C for 15 minutes, poured into glass petri-dishes and stored in a refrigerator until used.

Insecticides

Commercial formulated insecticides diluted on water in different concentrations were tested for their effect on the parasitoid *Bassus asper* Chou & Sharkey. We decided to use synthetically insecticides recommended by Aganon *et al.* (1997) against the host *M. vitrata*. Insecticides tested



were from different classes among the active ingredients. Tests were conducted according to standards made by the “International Organization for Biological Control” (IOBC). Five adults, two days old, were sprayed directly with 1 ml of different insecticide concentrations. Mortality was counted after 48 hours and the experiment repeated three times.

Data analysis

Concentration-mortality regressions were estimated by probit analysis with the statistical software SPSS, version 10. Data were not corrected for the analysis with Abbott’s (1925) formula, because control mortality was always below 4%.

Results

Four different parasitoids emerged from *M. vitrata* eggs and larvae collected in unsprayed fields of yardlong bean. The only egg parasitoid recorded was *Trichogramma evanescens* Westwood. *T. evanescens* hatched from a single collection in the second crop of 1999. Three species of parasitoids, *Exorista xanthaspis* (Wiedemann) and *Peribaea orbata* (Wiedemann), both family Tachinidae, and *Bassus asper* Chou & Sharkey, family Braconidae were recorded from bean podborer larvae and pupae. *B. asper* was the only parasitoid found in all five cropping periods, and therefore, was the most prevalent species observed from larvae and pupae. Parasitism in unsprayed fields of *V. sesquipedalis* on the CLSU campus was lowest (1.4%) in the wet season, 2000, and highest (17.1%) in the wet season, 1999 (Table 1).

Table 1 *Maruca vitrata* parasitized by *Bassus asper* in different seasons

Cropping period	Season	Rainfall (mm)		Larvae collected	Larvae parasitized
		Total	Per day		
19. May – 29. July 1998	Wet	634.5	8.6	462	66 (14.3%)
5. Jan. – 8. March 1999	Dry	15.0	0.2	240	12 (5%)
11. May – 19. July 1999	Wet	583.8	8.3	654	112 (17.1%)
5. Jan. – 11. March 2000	Dry	205.7	3.1	283	40 (14.1%)
15. May – 27. July 2000	Wet	865.1	11.7	641	9 (1.4%)

Table 2 Parasitism and parasitoids noted on *Maruca vitrata* at different locations, 1998-2000 in *Vigna sesquipedalis* fields treated and untreated with insecticides (*only one crop, 5 January to 8 March 1999)

Location	Insecticide treated	Parasitoid species	Parasitism (%)
CLSU	No	<i>B. asper</i>	11.5
		<i>E. xanthaspis</i>	
		<i>P. orbata</i>	
CLSU*	Yes	<i>B. asper</i>	5.1
		<i>E. xanthaspis</i>	
San Leonardo	Yes	<i>B. asper</i>	0.8
San Jose	Yes	<i>B. asper</i>	1.2

Mean parasitism was higher in untreated plots than in plots treated with insecticides (Table 2). Three species of parasitoids emerged from larvae collected in untreated fields, whereas only *B. asper* emerged from larvae collected in insecticide-treated fields located in San Leonardo and San Jose. *B. asper* and *E. xanthaspis* emerged from larvae collected in an insecticide-treated field at CLSU. The parasitoid *B. asper* was the only species found at all three locations.

All tested insecticides were toxic to *B. asper*. Chlorpyrifos and Carbaryl application resulted in the highest mortality.

Bassus asper was first described in 1992 by Chou & Sharkey in Taiwan. Current evidence indicates that *B. asper* is synonymous with *B. javanus* (Bhat & Gupta) (Fig. 1), and was described previously in Malaysia. Taxonomic revision of the two species is ongoing. A *Bassus*-species was recorded as a parasite on *M. vitrata* in Malaysia by Yunus & Ho (1980).

Table 3 Toxicity of different insecticides to *Bassus asper* adults after 48 h

Insecticide	Slope \pm SE	LD ₅₀ (ppm)	95% confidence	Recommended concentration (ppm) to control <i>M. vitrata</i>
Chlorpyrifos	0.064 \pm 0.009	100	65 – 161	590
Deltamethrin	0.492 \pm 0.067	44	25 – 74	140
Methomyl	0.063 \pm 0.007	468	276 – 730	800
Carbaryl	0.797 \pm 0.111	88	45 – 147	500



Figure 1 *Bassus javanus* (Bhat & Gupta) (photo by Andrew Polaszek)

Discussion

Although Barrion *et al.* (1987) recorded 17 parasitoids from larvae of *M. vitrata* in the Philippines, we identified only four, and two species of these, *T. evanescens* and *B. asper*, had not been recorded previously. *T. evanescens* was found only once emerging from eggs of the bean podborer. Because of experiments in surrounding fields with natural enemies of vegetable insect pests we suspect that *T. evanescens* was introduced.

The daily mean rainfall ranged from 0.2 and 3.1 mm during the dry season and 8.3, 8.6, and 11.7 mm during the rainy season. It appears that rainfall does not have a significant impact on *M. vitrata* mortality, because we collected high numbers of larvae during wet and dry seasons. Alghali (1993) found a positive correlation between cumulative rainfall and *M. vitrata* numbers on *V. unguiculata*. Because larvae feed inside flowers and pods they are probably protected from direct contact with rain.

Mean parasitism by *B. asper* in the wet season 2000 was low. It is unlikely that rain caused the low parasitism because in two earlier wet seasons parasitism was higher than in the dry season. We do not know what caused low parasitism in the first crop, 2000. However, our study indicates that the parasitoid complex associated with *M. vitrata* was the same in dry and wet seasons.

There may be several reasons why the larval parasitoids may not be efficient regulators of *M. vitrata* populations. First, mean parasitism was low in farmer fields treated frequently with insecticides. *B. asper* populations are negatively affected by insecticides used by farmers to control the host *M. vitrata*. The same insecticides have been found ineffective against *M. vitrata* (Ulrichs *et al.* 2001b). Secondly, *B. asper* attacks larvae but kills only pupae. Therefore larvae can continue to feed and damage a crop. Unfortunately, farmers are usually unaware of beneficial insects and continue to use insecticides.

Our data suggest, however, that parasitoids in general, and *B. asper* in particular, can contribute to the control of *M. vitrata* on *V. sesquipedalis* if insecticides are not used. Pest control strategies should foster the preservation of these and other natural enemies via the selection and judicious use of pesticides that have minimal impact on the natural enemy complex. Where possible, suitable habitats in and around yardlong bean fields should be provided to encourage parasitoid development and survival.

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ROLE OF NATURAL ENEMIES IN CONTROL OF RICE LEAF ROLLER, *PELOPIDAS MATHIAS* F. POPULATIONS IN THAILAND

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Abstract – Study on the role of natural enemies of rice leaf roller, *Pelopidas mathias* F. was carried out in Prachin Buri province in non-chemical treated wet season rice fields. Next natural enemies were detected: *Macrocentrus* sp., *Apanteles baolis* (Hymenoptera: Braconidae), *Goniozus* sp. (Hymenoptera: Bethyidae), *Halidaya* sp. (Diptera: Tachinidae) and fungies, which caused about 55.0% of *P. mathias* larvae mortality all together; particularly 17% from fungies, 16% – from *Macrocentrus* sp., 6% from *Apanteles baolis*, 6% from *Goniozus* sp. 5% from *Halidaya* sp., and 5% from total Tachinid + Braconid + Ichneumonid effect.

Key words: *Pelopidas mathias*, *Macrocentrus* sp., *Apanteles baolis*, *Goniozus*, *Halidaya*, natural enemies

Introduction

One of the most widespread rice field pests in Thailand is *Pelopidas mathias* F. White spherical eggs are laid by females singly on leaf blades. Larvae rest at the base of plants during the day and feed on leaf blades during the night. Young larvae roll portions of the leaf blade to make a shelter. Pupa are form in tubes which the larva made. No effective cultural control and resistant rice varieties are available against the skipper, *P. mathias*. Thus, effective management of *P. mathias* is possible only by using chemical treatments and biological control. Napompeth (1982) reported the next efficient parasitoids of *P. mathias* for Thailand: *Apanteles baolis*, *Argyrophylax nigritibialis*, *Charops bicolor* (Hymenoptera: Ichneumonoidea), and *Halidaya luteicornis* (Diptera: Tachinidae). Yasumatsu *et al.* (1980) also mentioned the effectiveness of parasitoids against pests of rice fields.

Materials and Methods

Weekly observations on rice fields were carried out from 40-days rice tillering stage until flowering stage (131 days). *Pelopidas mathias* larvae were randomly sampled in 4 non – chemical treated rice fields. Damaged leaves were randomly taken from each of 20 hills across the paddy. Each damaged leaf with *P. mathias* larva was put into separate tube for individual rearing of parasitoids.

Results and Discussion

Maximum number of *P. mathias* larvae was found on the 47th day, 30 larvae were picked during panicle stage. It was found, that *P. mathias* population in non-chemical treated rice field is higher at the beginning of rice tillering stage and later on this number always decreased; although pest's population sometimes fluctuates. However, *P. mathias* populations rarely have outbreak because of natural enemies influence.

The average mortality rate of *P. mathias* larvae caused by natural enemies is 55.0%, particularly from *Macrocentrus* sp. – 16%, *Apanteles baolis* – 6%, *Goniozus* sp. – 6%, *Halidayia* sp. – 5%, tachinids + braconids + ichneumonids – 5%, and fungi – 17%.

Maximum number

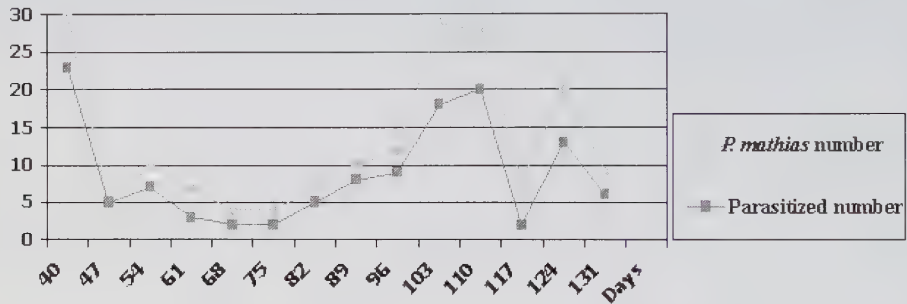


Figure 1 Ratio of non-parasitized and parasitized larvae of *Pelopidas mathias* in non-chemical treated, wet season rice fields in Prachin Buri Province in 1995



Conclusions

The highest observed density of *P. mathias* populations was six larvae per 20 hills at the rice tillering stage. During this period the larvae was 73.0% of *P. mathias* larvae were parasitized. Due to it, only 1.6 larvae per 20 hills left. It indicates that natural enemies can be very efficient in the control of *P. mathias* populations.

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The Department for Plant Protection and Soil Conservation of the Ministry of Agriculture and Regional Development established, by 1 January 1998, the Systematic Parasitoid Laboratory, a special laboratory of the Central Service for Plant Protection and Soil Conservation, working at the site of the Plant Protection and Soil Conservation Service of county Vas.

The main tasks are as follows:

- detection and determination of parasitoid species present in the cultivated crops,
- selection of the most effective parasitoid species for biological control,
- study and determination of their biology and host-parasite relations,
- analysis of the pest management programmes of different crops for host-parasite relations,
- study and use of techniques safe for the parasites,
- study of techniques safe for the parasites in the pesticide registration procedure, use of molecular biological methods, PCR for identification (taxonomy).



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